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A taxonomic revision of *Vermipardus* Stuckenberg, 1960, with descriptions of new species and notes on the biology and biogeography of the genus (Diptera: Vermileonidae)

by

B. R. Stuckenberg
(Natal Museum, P. Bag 9070, Pietermaritzburg, South Africa)

ABSTRACT

An analysis of the distribution of apomorphies among Afrotropical vermileonids shows the South African taxon *Vermipardus* Stuckenberg, 1960, originally described as a subgenus of *Lampromyia* Macquart, 1835, to warrant generic status. The genus is redescribed; a key is given to three species-groups and ten species; the following new species are described: *V. sylphe*, *V. londti*, *V. sathon*, *V. munroi*. Notes are given on adult phenology and the biology of the larval stages; the larvae make pitfall-traps in sheltered, mesic sites, and are opportunistic predators of small arthropods. The biogeography of *Vermipardus* is examined in terms of area cladograms derived from taxon cladograms for the *intermedius* and *brevirostris* species-groups, and against the background of geomorphological evolution of the Great Escarpment and the eastern slopes between the Drakensberg Mountains and the sea. The existence of a previously undetected endemicity centre involving northern Lesotho + Mont-aux-Sources is reported.

INTRODUCTION

Recent developments in systematic research on the Lower Brachycera have aroused new interest in the wormlion flies. Originally classified as a subfamily Vermileoninae of the Rhagionidae, the vermileonines were given family status by Nagatomi (1977) after a long period of uncertainty over their true relationships. In the following years, several authors attempted to place Vermileonidae more satisfactorily within revised classifications of the Lower Brachycera, but without achieving consensus or a conclusive result; summaries of this literature are given by Griffiths (1994) and Stuckenberg (1995). Failure to demonstrate a relationship between Vermileonidae and any other grouping of brachycerous families led Griffiths (1994) to erect the new infraorder Vermileonomorpha; this includes also the fossil families Eremochaetidae and Protobrachycerontidae.

This focus of attention on vermileonids underlines the need for new taxonomic studies. In most of the regional faunas the existing taxonomy is out of date. A revised taxonomy incorporating cladistic methodology would be advantageous for a better understanding of vermileonid biogeography. Brief summaries of the world distribution of the family were given by Wheeler (1930) and Hennig (1967), but an examination of vermileonid cladogenesis and evolutionary history remains to be done. The present study follows the description of *Vermilynx* Stuckenberg (1995) as a further contribution to improved knowledge of the exceptionally rich and diverse vermileonid fauna of Southern Africa.

This revision supplants my earlier work on *Vermipardus* (Stuckenberg, 1960), formerly described as a subgenus of *Lampromyia* Macquart and now accorded full generic status. The number of species is increased from six to ten, and it is now possible to identify three species-groups. Most of these new species reveal the existence of the *brevirostris* group, which is distributed in the midland and hinterland regions of Natal and in coastal parts of the Eastern Cape Province, from where almost no vermileonids had previously been recorded. An improved understanding of the biogeography of *Vermipardus* is also possible.

MATERIALS AND METHODS

The material comprises pinned flies, most of which are in the collection of the Natal Museum (NMSA). Specimens have been obtained from the Durban Natural Science Museum (DMSA), the South African Museum (SAMC, Cape Town), the Albany Museum (AMGS, Grahamstown), and the collection of Dr R. Miller (University of Natal, Pietermaritburg). Genitalia were macerated in hot KOH, dissected in water, and drawn with the aid of a camera lucida while mounted in glycerine jelly. Dissected genitalia are preserved in glycerol in a plastic microvial mounted on the staging pin. Wing photographs were taken with a WILD Photomicroscope. The proboscis:fore-femur ratio was obtained by dividing the length of the proboscis by the length (measured on its dorsal surface) of the fore femur.

The terminology employed for mesonotal patterning is illustrated in Fig. 4. The term 'delta-marks' is used for a pair of dark, elongated, subtriangular, posteriorly-attenuated markings that occur on the anterior part of the mesonotum in some species, one on each lateral declivity that bounds the median strip on which the median vitta or stripe lies. Standard morphological terminology is used, and label data are cited exactly as printed; a slash (/) indicates the end of a line of print, and two slashes (//) indicate information on a second label; supplementary information is given in square brackets [].

The following terminology is adopted for descriptions of the male genitalia: **synsternite (sn)** – the compound structure formed by the gonocoxites which are fused ventrally with one another and (presumably) completely with the hypandrium; **dorsal bridge (db)** – a transverse sclerite joining the dorsobasal edges of the gonocoxites, to which the aedeagus is attached and on which the proximal end of the proctiger articulates; **gonostyle (gs)** – termed dististyle previously; **ventral aperture (va)** – a ventromedian opening in the apical part of the synsternite, of specifically distinctive size and shape; **apical guide** (**ag**) – paired ventromedial extensions or elaborations of the posterior end of the synsternite, one on each side of the distal end of the ventral aperture, projecting posteriorly beyond the articulation sites of the gonostyles, approaching one another and thereby narrowing the distal end of the ventral aperture. Minute points (Fig. 28) which occur on the outer surface of the aedeagus in most species (see generic description below) are referred to as **spiculae** (Latin, *spicula*, fem. dim. of *spicum*, a point).

A summary of ascertainable proboscis:fore-femur ratios for all the species is given in Table 1. Only specimens in good condition were measured. In a few species an unusually large specimen of either sex proved to have an exceptionally long proboscis, evidently a result of allometric growth, which extended the range for these species; a case in point is *univittatus* whose ratio for females reaches 1.4 because of just one such specimen.

TABLE 1

Proboscis:fore-femur ratios of *Vermipardus* species (calculated ranges, based on specimens in good condition).

	♂♂	♀♀
basuto	1.4	–
brevirostris	–	0.5
brincki	1.1	–
intermedius	1.3	1.2
londti	0.8	–
munroi	0.6	0.6–0.7
promontorii	0.8–0.9	0.6–1.0
sathon	0.7–0.8	0.8
sylphe	1.2	1.1
univittatus	1.2–1.3	1.0–1.4

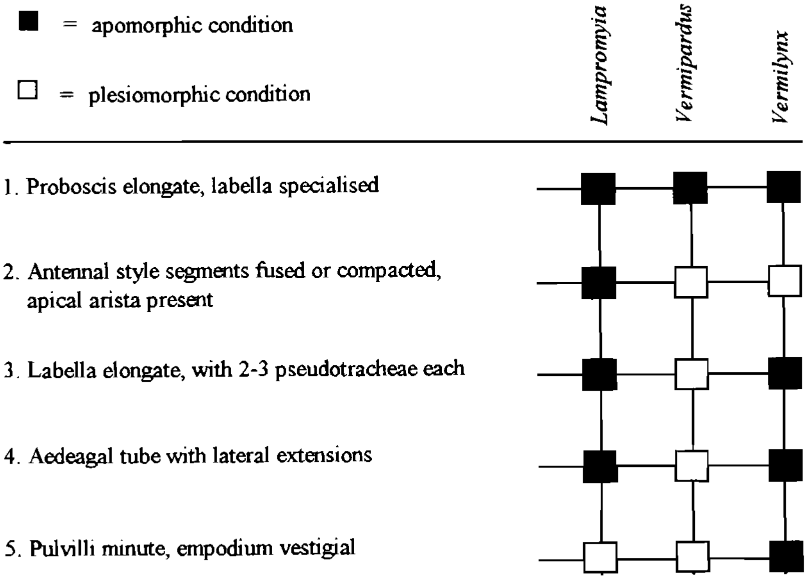
The material of Vermileonidae in most collections is very limited, probably because of a remarkable elusiveness on the part of these flies in the field. It is difficult to build up a series of any species from field-caught adults, except perhaps by the persistent use of Malaise traps. For this reason, resort is sometimes made to the rearing of larvae which may be easier to find. The flies may sometimes be found resting at or close to the site where they passed through their larval and pupal stages. After eclosion, the flies climb up nearby objects or surfaces and rest there until ready to fly. The type series of *Lampromyia (V.) promontorii* Stuckenberg consists of specimens netted from the roof of a small cave sheltering a patch of dry sand in which the larvae occurred. Experience has shown that flies caught in such situations, as well as those reared from larvae, may cause problems for the taxonomist because they were killed before their full colouration had developed. Teneral specimens can be recognised as such and put aside; they have an almost translucent integument, the wing lacks any pattern, and the hind tibiae may be slightly curved. It is the somewhat older but still immature specimens that may be perplexing.

Immature flies may have a paler, more translucent body colouring; species predominantly reddish-brown when mature appear more yellowish-brown, and dark markings on the mesonotum, pleura and abdominal tergites may be weaker and sometimes fugitive. The colouring of the hind legs is uniformly paler and close to that of other legs, with less contrast in species having a dark hind leg with a pale basal section. Melanistic species have less intense blackening of the integument, and there is much less contrast in any paler areas around the borders of the mesonotum, in the middle of the pleura, and basally on the abdominal tergites. Reared specimens, and those caught at breeding sites, should be kept alive for as long as possible before being killed and pinned.

TAXONOMY

When Bezzi (1926) provided the first account of South African Vermileonidae, he placed all the species known to him in the genus *Lampromyia* Macquart, 1835. The monograph by Stuckenberg (1960) increased the number of species considerably, with a new subgenus *Vermipardus* Stuckenberg described for a distinctive group of five species having a relatively shorter proboscis with more compact, laterally compressed labella, the antenna with an eight-segmented, non-aristate style, and the aedeagal tube without lateral extensions. Two further species of *Vermipardus* were described subsequently, *L. (V.) promontorii* Stuckenberg, 1961, and *L. (V.) vansoni* Stuckenberg, 1965.

The remarkable species *vansoni* was the subject of a recent study (Stuckenberg 1995) in which its distinctive characters were found to justify the erection of a new genus, named as *Vermilynx*. It was evident that *Vermilynx* has a closer relationship with *Lampromyia s. str.* than with *Vermipardus*. Important characters of these three taxa are analysed in Fig. 1. The following situation is evident:



■ = apomorphic condition

□ = plesiomorphic condition

	Lampromyia	*Vermipardus*	*Vermilynx*
1. Proboscis elongate, labella specialised	■	■	■
2. Antennal style segments fused or compacted, apical arista present	■	□	□
3. Labella elongate, with 2-3 pseudotracheae each	■	□	■
4. Aedeagal tube with lateral extensions	■	□	■
5. Pulvilli minute, empodium vestigial	□	□	■

Fig. 1. Distribution of certain apomorphic character-states in Afrotropical genus-group taxa of Vermileonidae. Plesiomorphic alternatives are described in the text.

Character 1: This is an apomorphy shared by all of the taxa; it is a synapomorphy of the Afrotropical Vermileonidae. The plesiomorphic condition is a short proboscis with large labella, as in *Vermileo* De Geer and *Ophiomyia* Yang.

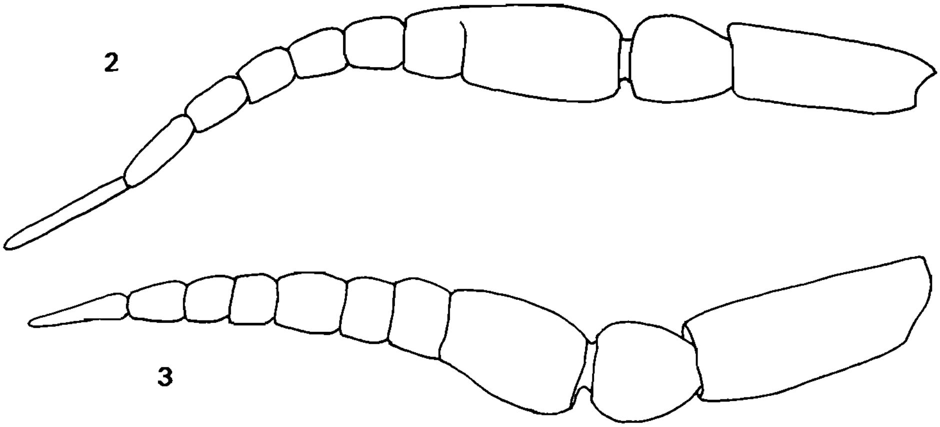
Character 2: This is an autapomorphy for *Lampromyia s. str.*; an arista is formed by either the apical stylomere or both the apical and preapical stylomeres together. The plesiomorphic condition is a tapering style in a graded series of eight segments.

Character 3: This is a synapomorphy for *Lampromyia s. str.* and *Vermilynx*. In the plesiomorphic alternative seen in *Vermipardus*, the labella are relatively small and laterally compressed, but with a greater number of pseudotracheae and nearer to the condition in *Vermileo*.

Character 4: This is a synapomorphy for *Lampromyia s. str.* and *Vermilynx*. In the plesiomorphic condition, the aedeagal tube lacks lateral extensions.

Character 5: This is an autapomorphy for *Vermilynx*. The plesiomorphic condition, found in all other vermileonid genera, is for the pulvilli and empodium to be small, but clearly present and subequal.

This analysis shows that, as previously constituted, *Lampromyia* inclusive of *Vermipardus* is paraphyletic. It follows that *Vermipardus* requires generic status. *Vermipardus* is the plesiomorphic sister-group of *Lampromyia* + *Vermilynx*.



Figs 2–3. Antennae of *Vermipardus* species. 2. *V. promontorii* (Stuckenberg). 3. *V. intermedius* (Stuckenberg). [In *promontorii* the apical and preapical segments are slender and elongate, as in most species of *Vermipardus*; these segments have a more plesiomorphic form in *intermedius*. Drawn from slide-mounted specimens; live flies have straight antennae.]

Key to Afrotropical genera of Vermileonidae

1 Antennal style comprising flagellum and seven style segments in a tapering unit, the apical segment often slender but not aristiform (Figs 2–3); proboscis:fore-femur ratio obviously less than 2.0; proboscis rigid, directed downwards 2

– Antennal style (Stuckenberg 1960: Figs 2, 3, 5, 6) with a variable number of segments fused with third segment, those segments not fused being shortened and reduced; apical stylomere long, slender, forming an arista in all species; in many species only apical and preapical stylomeres still free, in such cases preapical stylomere also slender and part of arista, though much shorter than apical stylomere; proboscis very elongate, clearly more than twice as long as fore-femur; proboscis capable of flexure in forward direction and posteriorly between legs .... **Lampromyia** Macquart

2. Proboscis more elongate, ratio 1.5–1.7; labella elongate tubular, dorsoventrally flattened in dried specimens, without setae; aedeagal tube with lateral extensions .... **Vermilynx** Stuckenberg

– Proboscis less elongate, length variable among species, ratio in known range 0.5–1.4; labella laterally compressed, short, subtriangular, bearing stiff setae; aedeagal tube lacking lateral extensions .... **Vermipardus** Stuckenberg

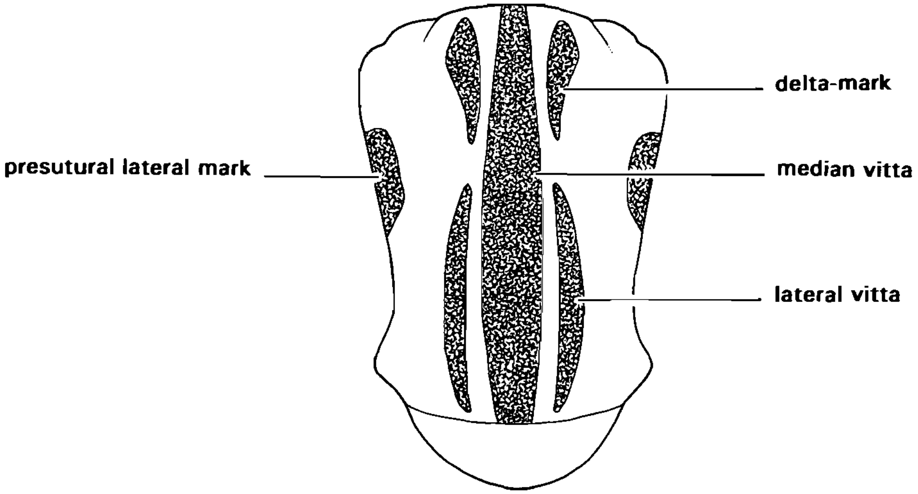
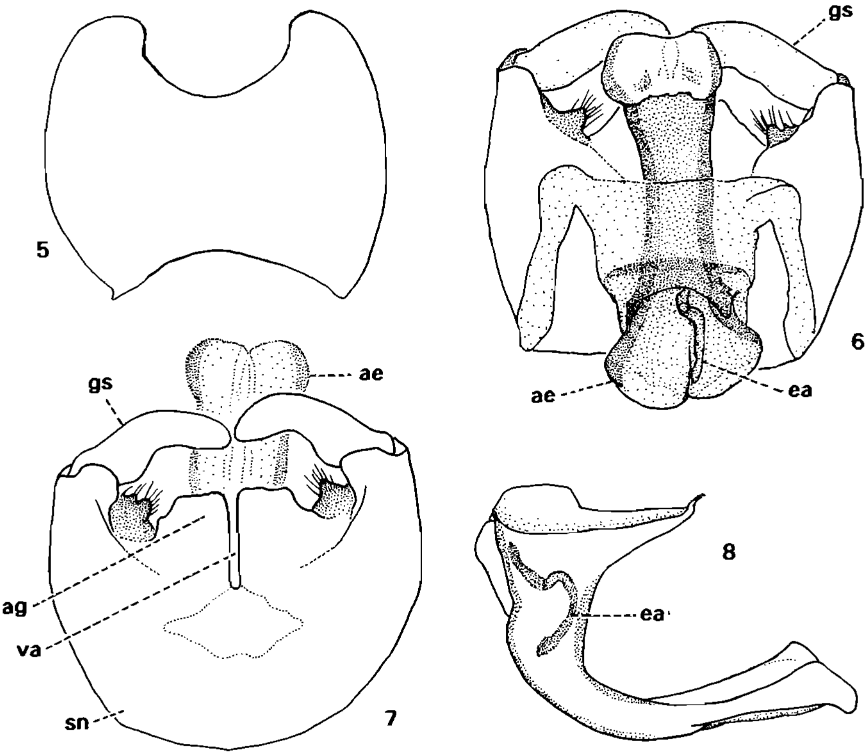


Fig. 4. Diagram illustrating nomenclature of components of mesonotal pattern in *Vermipardus*.

Vermipardus Stuckenberg, 1960, **stat. rev.**

Vermipardus Stuckenberg, 1960: *South African Animal Life* 7: 227 (as subgenus of *Lampromyia* Macquart, 1835). Type-species: *Lampromyia intermedia* Stuckenberg, 1955, by original designation.

Description: Head not sexually dimorphic; frons narrow, parallel-sided or slightly divergent towards ocelli; face narrow, progressively protuberant downwards; proboscis moderately to considerably elongate, proboscis:fore-femur ratio for known species spanning the range 0.5–1.4 (Table 1); proboscis rigid and straight; labella with short, stiff setae, subtriangular in lateral view, pressed together medially, in dorsal view forming a delta-shaped termination to proboscis, pseudotracheae numbering about 6 or 7 per labellum in species investigated, forming a short dendritic cluster (Stuckenberg 1960: Fig. 7); antenna (Figs 2–3) with eight-segmented tapering style, in occasional specimens of various species the basal and second style segments incompletely fused dorsally as in Fig. 2, terminal segment elongate and slender (except in *V. sylphe* sp. n., and of more plesiomorphic form in *V. intermedius*). Abdomen petiolate in male, weakly petiolate in female; female abdomen with nine tergites exposed. Male genitalia: dorsobasal margins of fused gonocoxites joined by a sclerotised dorsal bridge on which aedeagus is attached by its posterodorsal edge; gonocoxites almost completely united ventrally, hypandrium absent or completely fused with them; mediodistally the gonocoxites project posteriorly and partially enclose a ventral median aperture of specifically variable size; gonostylus inwardly articulating, moderately tapering, bifid in species of *brevirostris* group; epandrium broader than long, its basal margin concave; proctiger small, cerci scarcely protruding; aedeagus tubular, without lateral extensions, its base widened or flaring, its middle section directed posteriorly, apical section curved upwards, ventral keel rarely present on basal part, outer surface in most species with minute, flat, sharp, subtriangular, recumbent, sessile, distally-directed teeth (spiculae), sometimes these developed on margins of lateral flanges along aedeagal stem; ejaculatory apodeme a short, slightly flexed rod completely within basal part of aedeagus, its distal end attached to proximal end of membranous internal tube leading to aedeagal apex. Female genitalia: ninth tergite deeply arched, posteriorly forming a cowl or hood over proctiger; proctiger not extensible; cerci two-segmented, basal segment deeper than long, its posterior corners rounded, a sub-semicircular excision in hind margin in which the much smaller, short, squat second segment is placed; three subequal, spherical spermathecae; ninth sternite well sclerotised, transverse, posterior margin concave.



Figs 5–8. *Vermipardus promontorii* (Stuckenberg), ♂ genitalia. 5. Epandrium. 6. Hypopygium in dorsal view, epandrium removed. 7. Hypopygium in postero-ventral view. 8. Aedeagus in lateral view. [Abbreviations: ae = aedeagus, ag = apical guide, ea = ejaculatory apodeme, gs = gonostyle, va = ventral aperture.]

Key to species of *Vermipardus* Stuckenberg

1 Proboscis shorter than fore-femur, ratio 0.5–0.7; wing boldly patterned (Figs 44–46), R_{2+3} apically bent or curved forwards strongly; mesonotum (Figs 13, 14) with complex pattern including conspicuous delta-marks, median vitta extending onto scutellum; hind legs darker than other legs, hind tibia and basitarsus with contrasting pale basal section; ♂ gonostyle bifid (Figs 23, 29, 35), epandrium with large emargination in distal margin around proctiger (Figs 21, 25, 31); generally dark species (*brevirostris* group)..2

– Without that combination of characters; if dark species, delta-marks absent; if delta-marks present, species are reddish-brown or yellowish-brown; R_{2+3} more gently curved forwards apically except in *intermedius*, never angled there; if wing patterned, the markings less intensive; proboscis longer, ratio exceeding 1.0; ♂ gonostyle simple, not bifid; epandrium with relatively inconspicuous emargination in distal margin 5

2 Apical part of R_{2+3} strongly angled forwards, sometimes a small stump-vein at the angle; proboscis short (♂ 0.7–0.8, ♀ 0.8); scutellum dark medially, paler laterally; ♂ posterior emargination of epandrium squarish or subquadrangular – aedeagus elongate, its apex often exposed in dried specimens (Fig. 37), curving cephalad from dorsal bridge which is also elongate, resulting in an obvious ventral swelling of pregenital segments; ♀ abdominal tergites 2–4 mostly reddish-brown, dark markings on lateral margins only (assumed for *londti*) 3

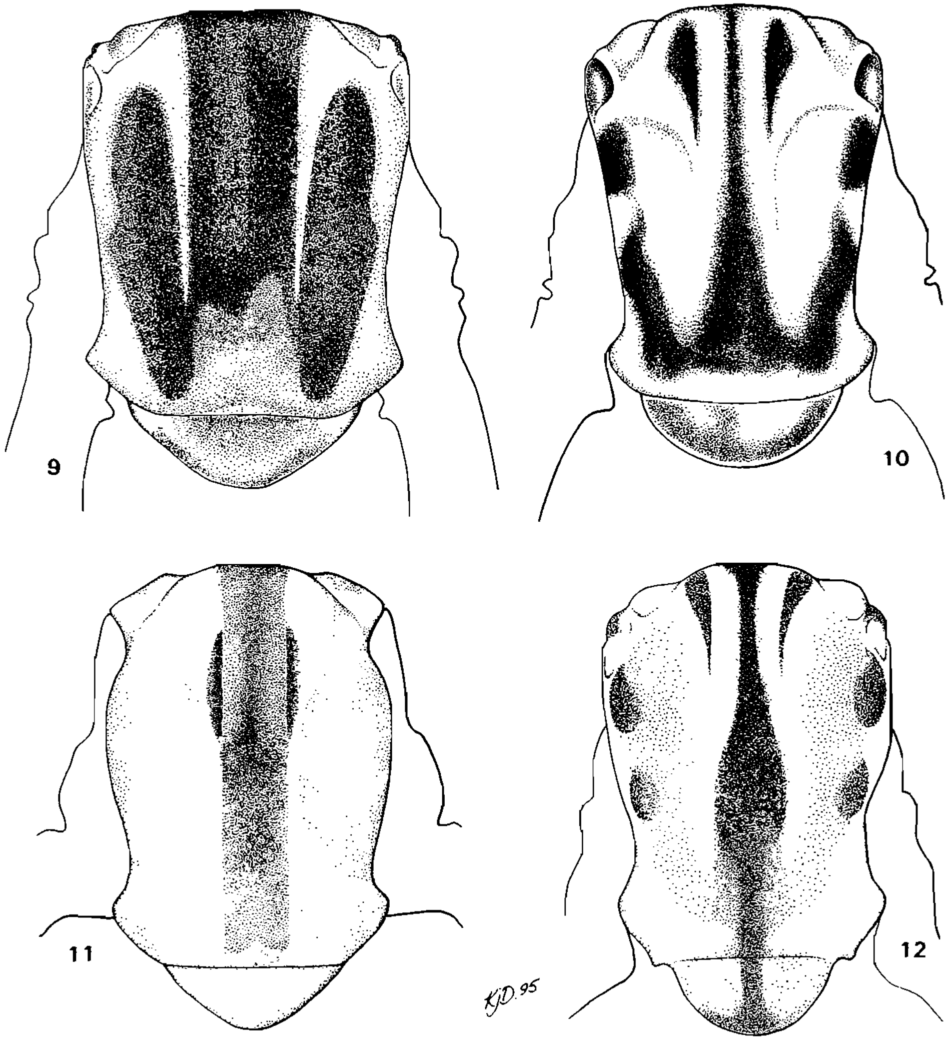
– Apical part of R_{2+3} strongly curved forwards; proboscis very short (♂ 0.5–0.6, ♀ 0.5–0.7); scutellum almost uniformly dark; ♂ posterior emargination of epandrium large and rounded – aedeagus not exceptionally elongate, pregenital segments not unusually enlarged ventrally; ♀ abdomen extensively blackish on tergites 2–4, with contrasting yellowish basal bands 4

3 ♂ abdominal tergites 2–4 of petiole shining blackish except for narrow basal reddish-yellow bands; dark markings of mesonotum not extending to lateral margins postsuturally; abdomen more moderately swollen below, this swelling not extending to sixth segment; gonostyle very asymmetrical, dorsal arm broadly expanded (Fig. 29); aedeagus unusually long, internally curved cephalad into segment 7 (♀ characters uncertain; Eastern Cape Province) ....**londti** sp. n.

– ♂ petiole segments not blackish but infuscated, with dull amber-yellow basal bands occupying about one-third of tergal length; dark markings of mesonotum extending to lateral margins postsuturally; abdomen progressively swollen ventrally to accommodate exceptionally long aedeagus which extends forwards into segment 6, aedeagus protruding prominently from end of abdomen in dried specimens (Fig. 37); gonostyle asymmetrically bifid, dorsal arm slender, curved and pointed (Fig. 35); tergites 1–6 with narrow, blackish posterior margins, also blackish on lateral margins, remainder reddish-brown (Natal midlands) .... **sathon** sp. n.

4 ♂ abdominal tergites 2–4 with basal yellowish bands over almost half of tergal length; ♀ with basal yellowish bands over about one-third of tergal length on tergites 2–4; ♂ genitalia (Stuckenberg 1960: Figs 47, 51, 61) with numerous distinctive features, notably form of aedeagus which lacks a basal midline flange on anterior surface, and has a pronounced curved recess on posterior surface below enlarged basal part (Natal midlands, Thukela River Basin)......................... **brevirostris** (Bezzi)

– ♂ abdominal tergites 2–4 with basal yellowish bands over about one-third of tergal length; ♀ with these bands short and weakly divided medially by a brownish infuscation; ♂ aedeagus and dorsal bridge more elongate (Fig. 20), aedeagus with a midline flange on anterior surface of base, and lacking a curved recess where stem of aedeagus emerges from flared base (Eastern Cape Province **munroi** sp. n.



Figs 9–12. Mesonotal patterns of *Vermipardus* species. 9. *V. promontorii* (Stuckenberg). 10. *V. intermedius* (Stuckenberg). 11. *V. univittatus* (Stuckenberg). 12. *V. sylphe* sp. n.

5 Predominantly dark species, mesonotum (Fig. 9) extensively occupied by a simple pattern comprising a broad median black vitta of uniform width, bordered on each side by a shorter black vitta which is incomplete anteriorly, a conspicuous narrow strip of silvery pruinescence between median and each lateral vitta; delta-marks absent; wing weakly fumose apically and in apex of second basal cell; scutellum uniformly dark; pleura variably coloured relative to age of specimen, more reddish-brown in immatures, extensively more melanistic and appearing bicolored in mature individuals (Cape Peninsula, *promontorii* group) 6

– Mostly reddish-brown or yellowish-brown flies, some species with delta-marks, always a median vitta on mesonotum but this not extending onto scutellum except in *sylphe*; wing without a definite pattern except in *intermedius*; all legs similarly coloured and more or less unicolorous (eastern half of South Africa, *intermedius* group) 7

6 Larger species (♂ wing 8.3–9.5 mm, ♀ wing 12.0 mm); frons longer than broad, with a low median swelling; head more dorsoventrally extended, ocelli clearly raised above eye-margin in lateral view; hind tibia blackish with pale whitish basal section, most of hind basitarsus whitish, darkened apically; epandrium flat, long, with large, subquadrate apical excision (Fig. 5), aedeagus (Fig. 8) apically bifid, completely lacking spiculae on outer surface ....**promontorii** (Stuckenberg)

– Smaller species (♂ wing 6.1 mm, ♀ wing 7.0 mm); frons about as broad as long, flat; head more rounded in lateral profile, ocelli hardly visible in lateral view; epandrium much shorter, flattened, with large curved posterior emargination; hind tibia brownish like femur; ♂ genitalia different in all respects, aedeagus not bifid apically, its middle portion with a row of strong subtriangular teeth on each side, appearing as toothed lateral flanges in ventral view (Stuckenberg 1960: Fig. 60) ....**brincki** (Stuckenberg)

7 Median vitta of mesonotum much narrowed anteriorly between conspicuous delta-marks (Figs 10, 12); fourth posterior cell open 8

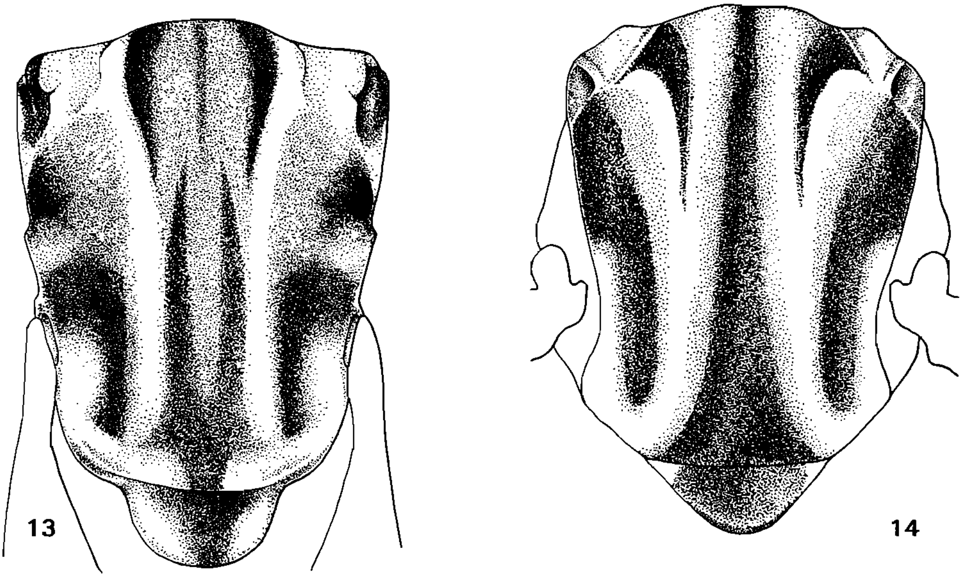
– Median vitta of mesonotum of uniform width, delta-marks absent or not clearly separated from median vitta (Fig. 11); fourth posterior cell usually closed (open in a minority of specimens of *univittatus*)..9

8 Antennal flagellum relatively large and thick (Fig. 16), only moderately tapering, apical segment short and small, shorter than preapical segment, not slender; mesonotum (Fig. 12) either with a presutural lateral mark, or this absent in immature specimens; median mesonotal vitta extending narrowly over median portion of scutellum and down postscutellum (not clearly evident in immature specimens); wing (Fig. 43) virtually unpatterned, R_{2+3} gently curved forwards apically (Natal Drakensberg) ....**sylphe** sp. n.

– Antennal flagellum (Fig. 3) tapering strongly, apical segment slender, about as long as preceding two segments together; mesonotum (Fig. 10) with subquadrangular dark mark adjacent to lateral margin immediately anterior to transverse suture; median vitta obscure in a few specimens, but in these the delta-marks and lateral marks conspicuous; scutellum and postscutellum not crossed by median dark stripe; wing patterned (Fig. 40), R_{2+3} strongly curved forwards apically (Eastern Cape Province).................**intermedius** (Stuckenberg)

9 Mesonotum with conspicuous dark spot laterally immediately anterior to transverse suture, and mesopleuron conspicuously dark (Fig. 15), in ♂ these marks intensely black; ♂ unusually hairy, occiput with many long hairs, mesonotal hairs longer than in other species, first tergite with long, recumbent hairs; ♀ thoracic pattern not as intense (available specimen possibly somewhat immature), these markings dark reddish-brown; dark markings on ♀ tergites 2–4 subquadrangular, large but not meeting in midline, remainder and tergites 5–7 yellowish-brown; boldly marked, strongly reddish-orange species (Lesotho) .... **basuto** (Stuckenberg)

– Mesonotum (Fig. 11) without a clearcut, dark lateral mark, its lateral margins broadly reddish- or yellowish-brown on each side of median vitta; vitta overlain by a narrow, paler, midline stripe of golden-brown pruinescence; pleura mostly reddish-brown, without contrasting dark marks; ♀ abdomen reddish yellow-brown, without dark markings except brownish postmortem blotching in some specimens, tergites without dark posterior margins (Katberg/Hogsback mountains of Eastern Cape Province, Drakensberg escarpment of Natal) .... **univittatus** (Stuckenberg)



Figs 13–14. Mesonotal patterns of *Vermipardus* species. 13. *V. sathon* sp. n. 14. *V. munroi* sp. n.

promontorii Group

Defined in couplet 5 of the key to species. The two included species are known only from the Cape Peninsula. They are confusingly alike, and their identification is further complicated by large variation in pleural colouring related to the degree of maturity of specimens. Their mesonotal pattern is closely similar, constant and distinctive. No morphological character could be found, however, that confirms a sister-group relationship. Indeed, the male genitalia are remarkably different, especially in the form of the aedeagus. In fact, the following character-states indicate that this may not be a monophyletic group: 1) the male genitalia of *promontorii* are unique in many features (see below); 2) *promontorii* has the hind-leg colouring seen in members of the *brevirostris* group; 3) *brincki* has the hind-leg colouring subdued and little different from that of the other legs, the ventral aperture elongate and narrow, the apical guides slender and projecting, and the gonostyles falcate, in these features resembling members of the *intermedius* group.

Vermipardus brincki (Stuckenberg), **comb. n.**

Lampromyia (Vermipardus) brincki Stuckenberg, 1960: 253–257.

Described on 1 ♂ holotype, 1 ♂ 1 ♀ paratypes, collected in a Malaise trap on Skoorsteenkop mountain overlooking Hout Bay. No other specimens have been seen.

Vermipardus promontorii (Stuckenberg), **comb. n.**

Lampromyia (Vermipardus) promontorii Stuckenberg, 1961: 120–124.

Apart from the type series, which was collected in a small cave on the slopes of Table Mountain overlooking Cape Town, only two other specimens can be recorded: 1 ♂ [SOUTH AFRICA] Table Mt/ Cape Town/ 2.xii.1927/ A.L. Bevis (NMSA); 1 ♂ South Africa W. Cape/ Cape of Good Hope/ Nat. Res. Olifantsbos/ nr. Skaife Centre/ 34° 16'S 18° 23'E// 18–19 September 1993/ S. van Noort/ Strandveld/ on coast at sea level/ Malaise trap (SAMC).

The latter specimen is fully mature and intensely melanistic; its abdomen is extensively blackish except for a narrow yellowish basal band on each of tergites 2–5; the pleura are mostly blackish, with an irregular, dull yellowish-brown zone obliquely across the middle. Its identification was uncertain until the genitalia were examined, as this specimen differs markedly in pleural colouring from the type series. It is now evident that the type series is immature; the specimens have the pleura largely honey-coloured yellowish-brown except for a darkish brown suffusion on the mesopleuron; the coxae and hind femora are yellowish-brown instead of blackish. In this species the proboscis is markedly short (Table 1).

The hypopygium originally illustrated was from a teneral specimen. Access to the mature specimen recorded above allows me to present new figures (Figs 5–8). This species is unique in the form of the ventral aperture and apical guides, in the presence of small, setose protuberances inward of the articulation sockets of the gonostyles, and in the form of the aedeagus, as well as its lack of spiculae.

Epandrium large, with broad, deep, curved apical emargination, posterior corners bluntly rounded and strongly curved under. Synsternite with very narrow, linear ventral aperture; a membranous area in ventral surface basad of ventral aperture. Gonostyles moderately curved inwards, bluntly rounded apically. Apical guides in form of straight-edged, squarish, transversely-placed flanges. A small, setose prominence present inwards of attachment of gonostyle. Aedeagus stout, with large, flaring, elongate base which has a small ventral keel; shaft relatively short, weakly sclerotised dorsally where there is a shallow trough which deepens apically, so that apex of aedeagus is a widely bifid, semi-membranous, expanded pad; spiculae absent. Dorsal bridge large, of indefinite form, weakly sclerotised. Ejaculatory apodeme a highly irregular, twisted rod.

intermedius Group

Defined in couplet 5 of the key to species, and at present including four species. The species are all distinctive, but *intermedius* is exceptional in its more elaborately patterned wing (Fig. 40), stronger apical flexure in R_{2+3}, and more complex mesonotal pattern (Fig. 10); in these characters it approaches species of the *brevirostris* group, but it differs from them notably in its longer proboscis (Table 1) and simple gonostyle.

The new species *sylphe* is enigmatic because of its antennal form (described in couplet 8); the antenna is unusually large (Fig. 16), and the small, simple terminal segment seems to be of a plesiomorphic type. The polarity of this antennal character state is unclear; if it is interpreted as plesiomorphic, *sylphe* would have a sister-group relationship with all other *Vermipardus* species, but no other characters could be found that confirm this. The form of the terminal segment is interpreted as a secondary reversion to an unspecialised state, and as an autapomorphy of *sylphe*. Features of the male genitalia indicate a relationship between *sylphe*, *basuto* and *univittatus*; this is consistent with the geographical contiguity in the distribution of these species (see biogeographical section below).

Vermipardus univittatus (Stuckenberg), **comb. n.**

Lampromyia (Vermipardus) univittata Stuckenberg, 1960: 257–258, 260.

This species was described on 3 ♂ from the Katberg mountain in the Eastern Cape Province and 1 ♀ from Grahamstown. The female is now considered possibly to have been mislabelled; the collector N. J. Myers was a student at Rhodes University, and he is known to have visited the Hogsback mountain (see below) where that specimen may in fact have been obtained.

The following record provides a predictable extension of the range of this species: 1 ♀ SOUTH AFR.: Cape Prov/ Hogsback 3226DB/ 13–20.xii.1985/ J. & B. Londt Forest/ & forest margins (NMSA). The Hogsback and Katberg mountains are on the contiguous Amatola and Winterberg ranges respectively. The species is now known also from the Drakensberg escarpment in Natal: 4 ♂ 4 ♀ SOUTH AFRICA. Natal Prov./ Drakensberg Mts (2929AD) Giants Castle Res. 5800 ft/ 1.xi.1972 ME Irwin; 1 ♀ Reared from/ larva collected/ at Giants Castle/ Natal/ emerged mid-May 1964; 1 ♀ Giants Castle/ Game Reserve/ Natal/ ME Irwin// Collected as larva/ emerged on 25 Oct. 1972 (all in NMSA).

Larvae from the Natal Drakensberg were sent by me to the late Dr Axel M. Hemmingsen who reared them successfully in Denmark; the flies are now in the University Zoological Museum, Copenhagen.

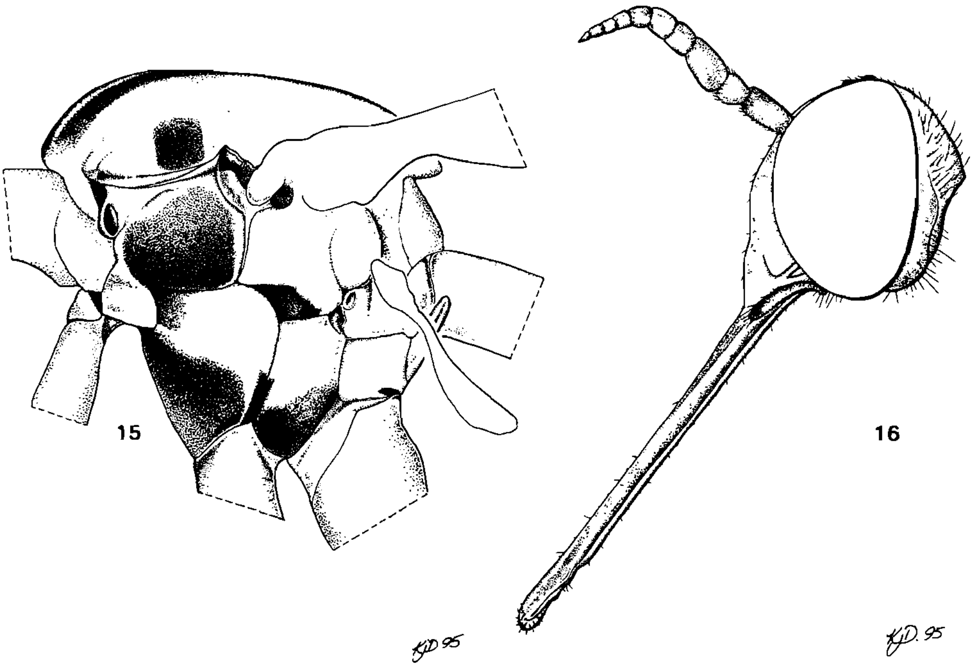
Vermipardus sp. *incertae sedis*

Lampromyia (Vermipardus) sp. *incertae sedis*, Stuckenberg, 1960: 264.

The identity of this male in DMSA, from Lidgetton in the Natal midlands, could not be conclusively determined previously. I have re-examined the specimen and now consider that it is probably a small, immature example of *univittatus*; its provenance in an upland region connected topographically with foothills around Giant's Castle makes this identification credible. The original figure of the epandrium of this specimen (Stuckenberg, 1960: Fig. 64) is incorrect and misleading; in shape, the epandrium matches that of *univittatus* (*op. cit.* fig. 52).

Vermipardus basuto (Stuckenberg), **comb. n.**

Lampromyia (Vermipardus) basuto Stuckenberg, 1960: 260–264.



Figs 15–16. Characters of *Vermipardus* species. 15. *V. basuto* (Stuckenberg), left side of holotype ♂ thorax, showing pattern. 16. *V. sylphe* sp. n., ♂ head.

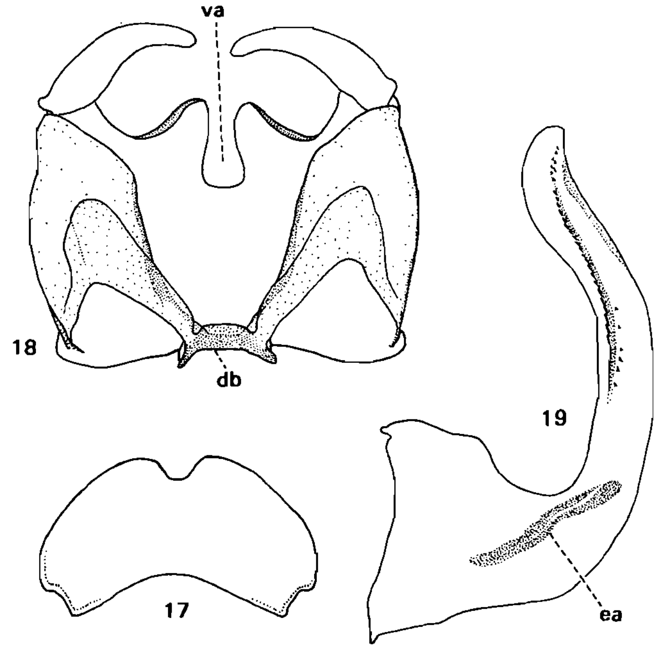
Still known only from the male holotype from Bokong and a female from Mamathes, in Lesotho. The male is highly distinctive on account of its rich colouring, strong pattern of bold black markings (Fig. 15), and abundant long hairs. The female is less intensely marked and may be relatively immature. Both specimens now lack the third segment and style of both antennae, so comparison with *sylphe* is not possible. No note was made in my original description of any unusual condition of the antenna, so probably *basuto* resembles other species of *Vermipardus* in having the apical stylomere slender and elongate.

Vermipardus intermedius (Stuckenberg), **comb. n.**

Lampromyia intermedia Stuckenberg, 1955: 263–265.
Lampromyia (Vermipardus) intermedia; Stuckenberg, 1960: 265–266.

This species is common in and around Grahamstown (Eastern Cape Province), its type-locality; the Albany Museum has 35 specimens sorted from Malaise trap catches made there by Dr F. Gess. On the evidence of the following two old specimens, the species occurs widely in the Fish River Basin: 1 ♀ [SOUTH AFRICA] Fort Beaufort/ Cape Province/ 10.x.1946/ J.S. Taylor (NMSA) – headless; 1 ♀ East London/ Lightfoot/ 1915 (NMSA) – one wing missing and most legs broken. The Fort Beaufort specimen has the anterior section of the median vitta faint between the delta-marks, and has venational abnormalities in both wings.

The Fort Beaufort record for *intermedius* is close to the Katberg and Hogsback localities where *univittatus* is recorded (q.v.), but these species probably have different habitat requirements and are unlikely to be sympatric; *univittatus* is a montane species, evidently preferring humid, forested localities.



Figs 17–19. *Vermipardus sylphe* sp. n., ♂ genitalia. 17. Epandrium. 18. Synsternite, dorsal view. 19. Aedeagus, lateral view. [Figures to different scales. Abbreviations: db = dorsal bridge, ea = ejaculatory apodeme, va = ventral aperture.]

Vermipardus sylphe sp. n.

Figs 16, 17–19, 43

Etymology: From *sylphes* (L.), a fairy-like spirit, in reference to the type locality and slender form of this species.

Material examined: All specimens are immature to some degree, having been reared from field-collected larvae. Holotype: ♂ [SOUTH AFRICA] [Drakensberg mountains] Fairy Glen/ Royal Natal National/ Park Sept. 1972/ B. Stuckenberg// Collected/ as larva/ emerged at/ Pietermaritzburg/ on 24 October 1972. Paratypes: 2 ♂ 1 ♀ , same data but emergence dates not recorded. All in NMSA.

Holotype ♂:

Head: Frons almost parallel-sided, at anterior end about one-fifth of greatest head width, uniformly ashy pruinose; ocellar tubercle dark shining brown; occiput ashy-grey, divided down midline by a brown stripe from ocellar tubercle to neck, a weak dark sepia mark adjacent to each upper eye margin; face translucent pale yellowish-brown, thinly silvery and pale golden tomentose; proboscis slender, elongate, moderately long, about twice greatest eye-height and a little longer than fore-femur (Table 1); antennae relatively elongate and thick, first segment pale brownish-yellow, pedicel light brownish, flagellum contrasting brown, apical flagellomere conspicuously small, shorter than preceding segment and of much smaller diameter at base.

Thorax: Mesonotum clear, warm amber-brown, patterned with dark brown as follows – a median vitta over entire length, this also extending narrowly over scutellum, vitta narrowing anteriorly over about half of its length, also narrowing posteriorly; a pair of delta-marks present; a subquadrate lateral mark just before transverse suture and adjacent to notopleural margin; a poorly defined sublateral postsutural mark; a conspicuous dark brown vertical line immediately anterior to spiracle below humeral callus; postscutellum shining amber-brown like mesonotum, obscurely darker brown medially. Pleura, coxae, fore and middle legs warm pale amber-brown, some obscure brownish underlying colour in mesopleuron, sternopleuron and hind coxa. Hind legs mostly smoky-brown, femur, tibia and basitarsus paler basally. Haltere stem pale on basal half, dark brown apically. Wing greyish-hyaline, almost without pattern, no stigma developed; 4th posterior cell widely open at wing margin in all specimens; apical section of R_{2+3} gently arching forwards to wing margin.

Abdomen: Strongly petiolate and slender, segment 3 much narrowed; tergite 1 mostly shining reddish-brown, tergites 2–5 with narrow basal amber-brown marks, remainder contrasting dark brown; tergites 6–8 and epandrium dark reddish-brown. Genitalia: Epandrium short, basal margin deeply curved, a distinctive small concavity at each basal corner, apical emargination very small. Synsternite with small subquadrangular ventral aperture, flanked posteriorly by deep, bluntly-rounded apical guides. Dorsal bridge projecting anteriorly to a level above basal edge of synsternite, small, narrow and short. Gonostyle simple, incurved. Aedeagus with long, laterally-compressed base, extending into a moderately upcurved stem which is margined laterally by a finely-sawtoothed ridge, some spiculae on shaft basad of basal termination of ridge.

Paratype ♀ :

Generally resembling male, abdomen less slender. Mesonotum with slender, irregular sublateral stripes in place of the 2 pairs of sublateral marks in ♂; basal half of tergite 2 brownish-yellow, contrasting with blackish-brown on apical half; remaining tergites with irregular reddish-brown lateral marks, medially broadly darkened, postmortem changes obscuring pattern; apically the abdomen extensively dark brown. Wing membrane shining greyish-hyaline, slight pale brown infumescence in costal and subcostal cells.

Wing length: ♂ 5.9–7.0 mm; ♀ 8.6 mm.

Notes: The type locality, Fairy Glen, is a small, thickly wooded valley close to the staff offices at the entrance to the Royal Natal National Park.

brevirostris Group

This group was not identified in my earlier study (Stuckenberg 1960); at that time only the species *brevirostris* was known.

Defined in couplet 1 of the key to species; the species are distinctive on account of their boldly patterned wing and thorax, and the strong colouring of the hind legs. The monophyly of this group is demonstrated by two apomorphies: the bifid gonostyles, and the strong apical flexure of R_{2+3}; the short proboscis is also characteristic. The four known species form a graded transformation series in respect of an extraordinary elongation of the aedeagus, with associated extension of the dorsal bridge; the most extreme elongation is in *sathon* and *londti*.

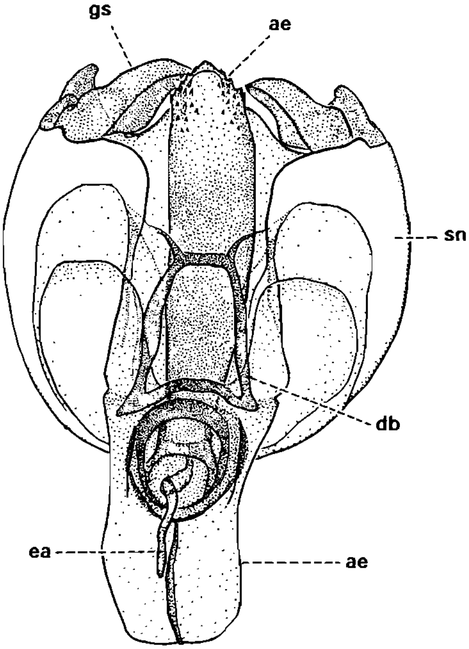


Fig. 20. *Vermipardus munroi* sp. n., hypopygium in dorsal view, epandrium removed. [Abbreviations: see captions for Figs 5–8, 17–19.]

Vermipardus brevirostris (Bezzi), **comb. n.**

Lampromyia brevirostris Bezzi, 1926: 303–304; Stuckenberg, 1955: 265.
Lampromyia (Vermipardus) brevirostris; Stuckenberg, 1960, 266–267.

For many years the only certain representative of this species was the holotype (in SAMC) collected at Mfongosi in the Thukela (Tugela) River valley of Natal. In his account of the species, Bezzi recorded a male from East London collected by the late H. K. Munro, but it could not be located in the South African Museum. Subsequently, the specimen, bearing Bezzi's label, was found in the Diptera collection of the Transvaal Museum when this was donated to the Natal Museum. It proved to be one of a series which in fact represents a new species closely similar to *brevirostris*, described and named below as *V. munroi* sp. n.

I discovered a larval population of *brevirostris* in valley-bushveld near Estcourt; this locality is in the drainage basin of the Thukela River. The following specimens were reared: 1 ♂ 1 ♀ [SOUTH AFRICA] Rensburgspruit/ Farm near/ Estcourt, Natal/ Valley Bushveld/ Stuckenberg// Larva collected/ 22.11.94. Adult [♀]/ emerged 25.1.95// Larva in hole/ in riverbank [Rensburgspruit River, a tributary of the Bushman's River]/ near farmhouse [of Mr D. Green] (NMSA). The male was found freshly dead during January 1995, having failed to complete eclosion.

This species and *munroi* have a very short proboscis (Table 1). The epandrium has a large semi-circular posterior emargination which can be seen without dissection. The aedeagus (Stuckenberg 1960: Fig. 61) is distinguished by the deep curved recess below the enlarged basal part, and by the row of strong teeth ventrally on each side of the stem. The synsternite has a large ventral aperture and narrow, subacuminate apical guides. The dorsal bridge is unmodified in comparison with other species of the group.

Vermipardus munroi sp. n.

Figs 14, 20–24, 46

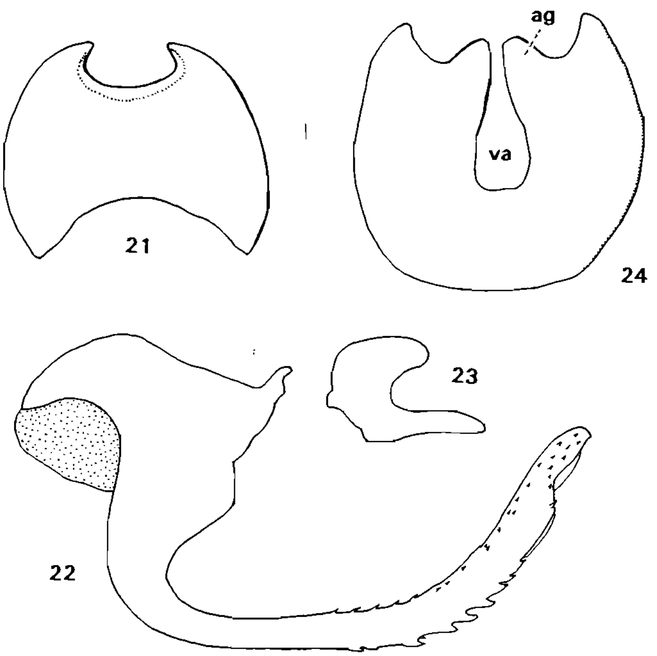
Etymology: Named in honour of the late Dr H. K. Munro, collector of the type material and a specialist on Tephritidae for more than 50 years.

Material examined: Holotype: ♂ [SOUTH AFRICA] East London/ 27.2.25/ H. K. Munro. Paratypes: 1 ♂ 3 ♀, same data, collecting dates – ♂ 27.2.25, ♀ ♀ 29.1.25, 20.2.25, 25.2.25. One specimen bears a label in Bezzi's handwriting: 'Lampromyia brevirostris Bezz ♂'; it is a female. Bezzi misread the date on Munro's label as 25.12.23; the date is 25.2.25. All in NMSA.

Holotype ♂:

Head: Frons slightly divergent towards ocelli, at anterior end about one-seventh of greatest head width, silvery-brown pruinose; ocellar tubercle shining dark brown; occiput thinly silvery-grey pruinose, minutely flecked with reddish-aureous, a fugitive dark brown, laterally tapering mark against upper orbit on each side, and a broad, poorly defined brown area extending from posterior end of ocellar tubercle to neck; face translucent, very pale yellowish, thinly pale-golden setose; palps and labrum clear light brown, proboscis dark, distinctly short, slightly longer than eye-height, a little more than half length of fore-femur (Table 1); antennal scape pale yellowish-brown, lightly suffused with brown apically and on upper and lower margins in lateral profile, pedicel similar but shifting brownish suffusion more extensive; antennal style strongly tapering, apical stylomere very slender, all segments uniformly brownish, contrastingly darker than scape and pedicel.

Thorax: Mesonotum shining light brown, strongly patterned with dark brown as follows: a median vitta along entire length, also extending across scutellum, narrowing anteriorly, broadest posteriorly, at anterior end this vitta joining a shining brown area on anterior face of thorax; a pair of prominent delta-marks, these also joining brown anterior face of thorax; a vertical, blackish-brown line immediately anterior to spiracle, below humeral callus; a large mark against notopleural margin, bordered posteriorly by transverse suture; a poorly-defined lateral vitta above supra-alar declivity, postsutural part of mesonotum thus appearing trivittate; postscutellum pale shining brown. Mesopleuron, lower half of sternopleuron, and pteropleuron medium brown; upper sternopleuron and hypopleuron pale yellowish. Fore and middle legs strongly yellowish-brown, mid-coxae brownish over apical half, darker towards apex; hind coxae mostly dark brown, grading rapidly to yellowish-brown



Figs 21–24. *Vermipardus munroi* sp. n., ♂ genitalia. 21. Epandrium. 22. Aedeagus in lateral view. 23. Left gonostyle in posterior view. 24. Synsternite in ventral view.

basally; hind femur warm light brown over most of its length, a very short basal section pale, a short apical portion darker brown; hind tibia darker shining brown, except for short whitish basal section; hind basitarsus whitish, tarsomeres 2–5 progressively more darkly infused with brown towards end of leg. Haltere knob dark brown, apical half of stem brown, basal half creamy-white. Wings hyaline, with strong clear yellowish-brown pattern; apical brown mark separated from brownish base of marginal cell, no stigma developed; 4th posterior cell closed in both males; apical section of R_{2+3} strongly curved forwards apically.

Abdomen: Strongly petiolate, slender and glossy, segment 3 much narrowed; tergites 2–3 darkish brown except for strongly contrasting yellowish transverse band over about basal third; tergite 4 mostly brownish, with short yellowish basal band; remaining tergites brown with some dark postmortem blotching. Genitalia: Epandrium strongly arched, apical emargination large, prominent and deeply curved. Synsternite with large ventral aperture which is subpyriform with extended, posteriorly-narrowed neck between apical guides which are simple, broad, bluntly rounded lobes. Gonostyle bifid, upper arm a short, stoutly ovate lobe, lower arm much narrower, longer, finger-like. Dorsal bridge a sclerotised trapezium narrowing posteriorly, with strong membranous connections laterally to dorsal surfaces of synsternite. Aedeagus strongly curved, its base recurved cephalad, extended as a midline keel ventrally; shaft slender, strongly flexed upwards, its lower edge on each side with strong, posteriorly-directed teeth, spiculae scattered on upper surface of upcurved portion.

Paratypes ♀ :

Generally resembling male; abdomen mostly dark brown, tergites 2–4 with conspicuous dull yellowish basal bands over about apical one-quarter or slightly more of tergal length, these bands weakly and incompletely divided medially by brownish suffusion; apically the abdomen very dark brown. Pleura and mesonotum with paler areas stronger brown than in males, possibly due to greater maturity; 4th posterior cell closed in all specimens; wing pattern variable in that a pale, subtriangular area is sometimes enclosed in brown mark in apical part of first submarginal cell.

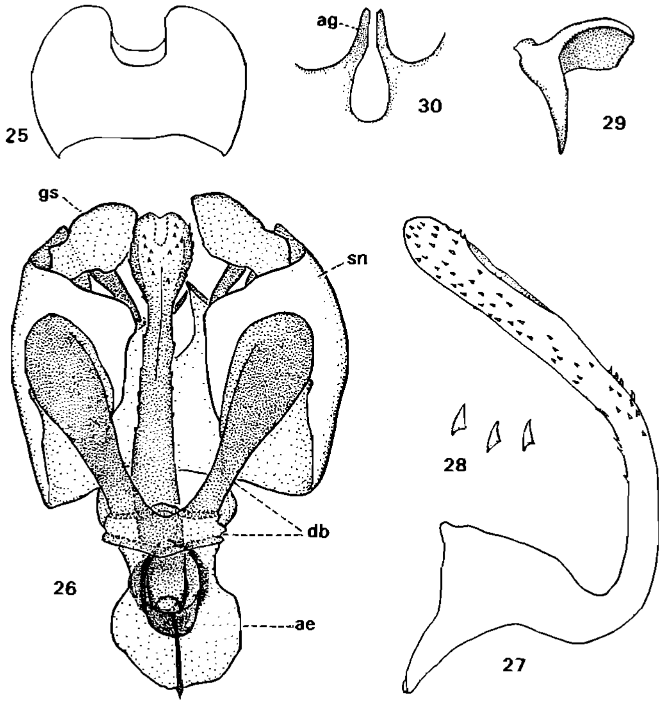
Wing length: ♂ 7.8 mm (both specimens); ♀ 9.2 mm (two specimens, third has damaged wingtips).

Notes: Unfortunately the labels give no information about where in East London the type series was collected. The species may frequent the small wooded valleys that are numerous on the coastal plain in that district.

Vermipardus londti sp. n.

Figs 25–30, 44

Etymology: Named in honour of Dr Jason Londt, collector of the holotype and a distinguished specialist on Afrotropical Asilidae.



Figs 25–30. *Vermipardus londti* sp. n., ♂ genitalia. 25. Epandrium. 26. Hypopygium in dorsal view, epandrium removed, stippled to emphasise form of dorsal bridge. 27. Aedeagus in lateral view. 28. Spiculae enlarged. 29. Left gonostyle in posterior view. 30. Ventral aperture and apical guides of synsternite.

Material examined: Holotype: ♂ SOUTH AFR[-ICA]: Cape Prov [-ince]/ Boesmansriviermond/ 3326AD 27–31.xii/ 1985 J. Londt Hill/ above caravan park (NMSA). Paratypes: 2 ♂ [E. Cape Province] Groot Rivier, Knysna District, Dec.1955, Martin; 1 ♂ Walmer, P.E. [Port Elizabeth], 1–17.I.1969, E. Gess (AMGS). A pest-damaged female in AMGS with the same label data as the Groot Rivier paratypes is probably conspecific.

Holotype ♂:

Head: Frons, face and occiput thickly golden-brown pruinose; frons narrowly blackish anteriorly, slightly divergent posteriorly, width at anterior end about 18 % of head width; ocellar tubercle shining blackish; occiput bordered above along each eye-margin by dark velvet-brown pruinescent strip that widens towards vertex; a patch of similar colour above neck and extending to ocellar tubercle; antennal scape and pedicel dull brownish-yellow, flagellum contrasting dark brown except for narrow pale zone at base of basal segment; palps and proboscis blackish; proboscis short, about one-quarter of eye-height, shorter than fore-femur (Table 1).

Thorax: Mesonotum warm yellow-brown, strongly patterned as follows: median vitta blackish-brown in postero-dorsal view, becoming sepia-brown in oblique lateral view, overlain with shining reddish-aureous pruinescence, tapering and fading somewhat anteriorly, posteriorly attaining hind margin of mesonotum; strong black delta-marks present, extended posteriorly as silvery-grey pruinescent stripes bordering median vitta; a presutural, subquadrate, lateral dark brown mark bordering notopleuron; postsuturally is a lateral dark brown stripe, posterior part of mesonotum appearing trivittate; a strong vertical black line anterior to spiracle, below humeral callus; scutellum darkened centrally, with yellowish-brown borders and darkened lateral corners. Pleura distinctly bicolored, shining dark brown on mesopleuron, pteropleuron, and lower half of sternopleuron and hypopleuron, a creamy-brown band occupying upper sterno- and hypo-pleura; middle and hind coxae blackish-brown, fore-coxae dull dark yellowish-brown. Fore and middle femora dull yellowish-brown, tibiae paler, tarsi darkened progressively apicad, basally the basitarsi coloured like the femora. Hind legs relatively stout, femur and tibia distinctly swollen apically; femur dark brown except proximally where it pales progressively to a pale smoky-brown at extreme base; tibia mostly strong blackish-brown, except for short, pale smoky-brown section at base; basitarsus creamy-brown over basal half, apical half and all of tarsomeres 2–5 blackish-brown. Metanotum shining dark brown medially, yellowish-brown laterally. Haltere stalk mostly creamy-brown, apically infuscated, knob blackish. Wing membrane smoky-grey, costal cell brownish; strong brown pattern present as figured, a clear patch enclosed by brown in apex of 1st submarginal cell, brownish patch irregularly present in apex of 1st basal cell; fork of R_4 and R_5 wide, R_4 curved sinuously forward; 4th posterior cell closed and stalked, in one paratype closed at wing-margin.

Abdomen: Strongly petiolate over third segment; tergites shining blackish-brown with contrasting short brownish-yellow basal bands on tergites 2–5, tergites 1 and 6–7 entirely dark. Genitalia: Epandrium short, with deep, squarish apical emargination flanked by broadly rounded posterior corners. Synsternite with small, narrowly ampulliform ventral aperture. Apical guides elongate, slender, closely approaching one another. Gonostyle bifid, strongly asymmetrical, upper branch a broad, curved, transverse lobe with an almost straight, microserrate inner margin; lower arm narrow, straight, pointed. Dorsal bridge strongly sclerotised, in form of V with truncated base, lateral arms expanded over area of attachment to upper surfaces of synsternite; bridge extending cephalad of basal margin of synsternite to accommodate extended aedeagus. Aedeagus protruding prominently between cerci in dried specimens; elongate over its upcurved apical portion, in dorsal view tapering before expanding into enlarged apex; base flaring moderately, keel absent; shaft narrow, with many spiculae scattered over dorsolateral and lateral surfaces, and a short row of strongly projecting teeth on each side of ventral surface.

Paratypes ♂:

Proboscis length variable, 1.4 to 1.5 times eye-height.

Wing length: ♂ holotype 6.4 mm, ♂ paratypes 6.0–6.7 mm.

Notes: The range of this distinctive, strongly patterned species may extend further westwards than present records indicate.

Vermipardus sathon sp. n.

Figs 13, 31–37, 45

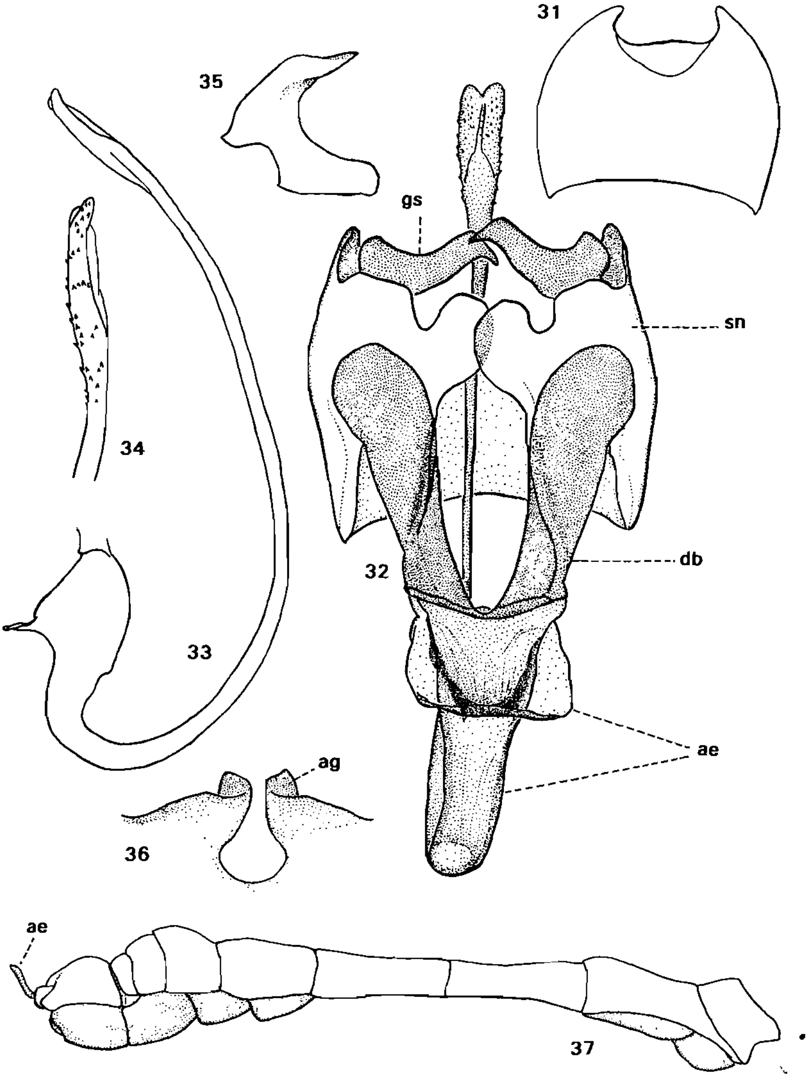
Etymology: Gr. *sathon* = one with a large penis, in reference to the extraordinarily elongate, protruding aedeagus.

Material examined: Holotype: ♂ SO [SOUTH] AFRICA: Natal/ Ashburton [east of Pietermaritzburg]/ October 1980/ R.M. Miller Mal.[Malaise] Trap. Paratypes: 4 ♂, same locality, coll. J. C. Manning, April 1981 (all in NMSA). 1 ♀, S. AFRICA: Natal # 10G/ Midlands. Howick/ 29°29'S. 30°13'E 1060 m/ Date: 3.X.1992/ Coll. K. E. Whittington. All in NMSA.

Holotype ♂:

Head: Frons slightly divergent towards ocelli, width at anterior end one-sixth of head width; frons, face and occiput densely shining yellow-brown pruinose; frons with apruinose greyish lateral strips and a small, irregular, median, brown mark anteriorly; ocellar tubercle shining blackish-brown, connected to neck by a thin, dark line, a short, dark sepia-brown triangle at upper part of each orbit adjacent to vertex; on each side of occiput is a fugitive spot of dark brown, this appearing to enlarge and changing in intensity when specimen is moved to a more oblique dorsal view; antennal scape and pedicel dull yellowish-brown, style dark brown except for paler base of basal segment; labrum and palps brown, labium dark brown; proboscis length about equal to eye-height, about three-quarters length of fore-femur (Table 1).

Thorax: Mesonotum with warm yellowish-brown underlying colour, heavily patterned with dark sepia-brown as follows: complete median vitta present, narrowing anteriorly between a pair of elongate delta-marks, narrowed anterior part of vitta bordered by paler, reddish sepia-brown with which fugitive anterior end appears to merge as specimen is moved into anterodorsal view; vitta bordered laterally by strip of shining silvery-grey pruinescence, these strips also bordering



Figs 31–37. *Vermipardus sathon* sp. n. 31-36. ♂ genitalia. 31. Epandrium. 32. Hypopygium in dorsal view, epandrium removed, stippled to emphasise form of dorsal bridge (db), aedeagus (ae), and gonostyle (gs). 33. Aedeagus in lateral view (75 % of scale of Fig. 32). 34. Apex of aedeagus in lateral view, enlarged to show distribution of spiculae. 35. Left gonostyle in posterior view. 36. Ventral aperture and apical guides. 37. ♂ abdomen in lateral view, showing swollen ventral area of terminal segments and protruding aedeagus. [Abbreviations: see captions for Figs 5–8, 17–19.]

diverging outer edges of delta-marks; declivous sides of mesonotum extensively darkened, a paler area where traversed by transverse suture; postsuturally appearing trivittate. Scutellum transversely rugose, blackened on disc, laterally dull yellowish-brown. Postscutellum extensively shining dark brown. Pleura: mesopleuron, pteropleuron, and lower halves of sternopleuron and hypopleuron, shining dark brown, an obscure band of dull yellowish-brown across upper sternopleuron and hypopleuron. Mid and hind coxae mostly dark brown, more blackish on posterior surfaces and on lower margins, paler basally, with thin overlying pubescence of minute recumbent golden hairs; fore coxae similar but paler. Fore and mid trochanters dark, remainder of fore and mid legs uniformly warm yellowish-brown apart from brownish infusation on apical three tarsomeres. Hind femur clear shining brown, darkened over a short apical section; hind tibia with short pale basal section, mostly brown like femur, darkening gradually apically, tarsus darkish brown, paler over basal third of basitarsus. Wing with 4th posterior cell closed in all specimens; R_{2+3} with strong apical bend, this sometimes asymmetrically variable to a small extent in some specimens, most wings of the type series with a definite angle at the bend, and some with a short stump-vein at the angle; R_4 strongly sinuous; pattern like that of *londti*, membrane greyish-hyaline.

Abdomen: Moderately petiolate, markedly swollen after segment 4 due to retro-elongation of aedeagus; first tergite brownish-black over most of sides, this colour extending over median part as a narrow transverse band; tergites 2–5 each with a bare, clear yellowish-brown basal third or more, remainder more brownish-yellow, darkly haired, and darkened laterally; tergites 6–8 and epandrium dark brown; hypandrium yellowish-brown, darker on lateral margins, palest midventrally; aedeagus protruding prominently upwards between cerci. Genitalia: Epandrium large, longer than in *londti*, apical emargination short but broadly subrectangular, posterior corners narrow, lateral margins strongly curved. Synsternite with small, subpyriform ventral aperture; inner posterior margins expanded as 2 lobes closely adjacent in midline (shown overlapping in Fig. 32, an artefact). Apical guides small, laterally flexed, squarish flanges. Gonostyle bifid, strongly asymmetrical, upper arm in dorsal view with a short, sharp, inflexed point; ventral arm a ventrally-directed, incurved flange. Dorsal bridge massive in proportion with enormously elongate aedeagus; in form of a strongly sclerotised V with truncated base and apically rounded arms where attached to synsternite, whole structure extending far cephalad into abdomen. Aedeagus protruding prominently between cerci; extremely elongate, slender, arched, its base flexed upwards; apex expanded over a short length and bearing spiculae.

Paratype ♀ :

Relatively robust in comparison with ♂; patterning of head, thorax, legs and wings as in ♂, but colouring more intense, and median vitta even more fugitive between delta-marks. Abdomen: first tergite reddish yellow-brown, darkened by a transverse blackish band that is strongly constricted medially; tergite 2 dark yellow-brown basally and centrally, on each side a blackish mark that is widest anteriorly and tapers posteriorly, hind margin with a transverse blackish band broadly separated from lateral markings; tergite 3 evidently similar to tergite 2, but colouring obscured by postmortem changes, generally dark reddish yellow-brown anteriorly and centrally, darkened on lateral and posterior margins; tergites 4–6 mostly dark reddish yellow-brown, narrowly darkened on hind margin, sides darkened but this not clearly defined; tergites 7–8 dark brown with obscure blotching.

Wing length: ♂ holotype 6.1 mm, paratypes ♂♂ 6.3–6.5 mm, ♀ 8.3 mm.

Notes: Dr Miller informs me that the holotype was caught in a Malaise trap set across a dry streambed in valley-bushveld in the 'Lion Park' nature reserve east of Ashburton. This is topographically complex terrain, in places thickly bush-covered, descending steeply to the Valley of a Thousand Hills in the Umgeni River Basin.

NOTES ON THE BIOLOGY OF *VERMIPARDUS*

Hardly anything is known about the biology of *Vermipardus* flies. Their elongate proboscis appears to be adapted for nectar-feeding; evidence for this is seen in the occasional presence of pollen grains on pinned specimens, but I am not aware of any records of these flies being seen on flowers. Reared captive flies show a restless, energetic behaviour as soon as firming of the exoskeleton and wings has been completed after eclosion. This may be evidence of a dispersal phase that would occur under natural conditions, when mates are located away from the site of larval development, and when oviposition may occur. The scattered nature of larval colonies suggests that such a dispersal episode probably occurs, though it is also probable that some flies oviposit in the same site where they passed through their immature stages.

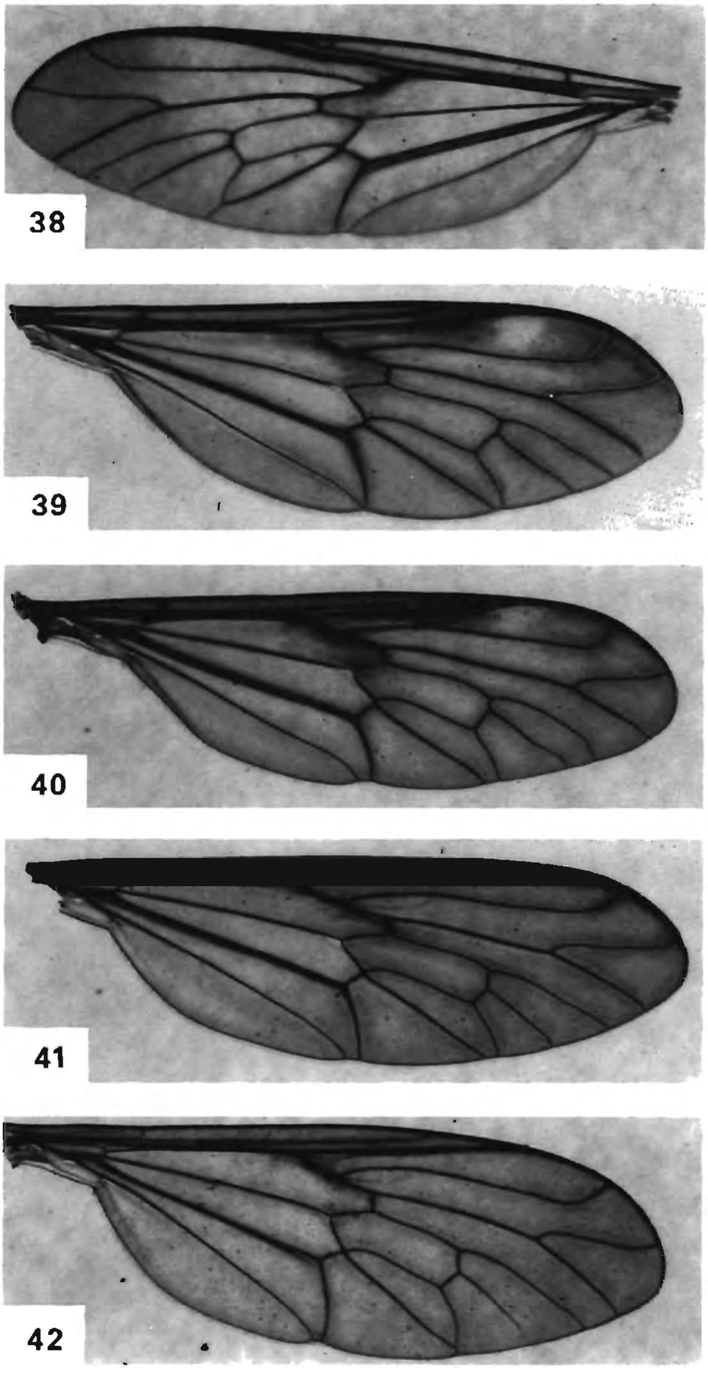
In Table 2 the data on adult phenology are summarised by the month; any month for which there is only a record based on a reared specimen is indicated, as it is not yet known whether such records always correspond to times of adult occurrence in nature. If no distinction is made between rearing and field-based records, the following conclusions can be drawn: 1) There are two peak periods in the year: (a) September–November (spring to early summer), with a peak in October (5 species); and (b) December–February (summer), with a peak in December (5 species). The two species of the *promontorii* group appear respectively in these two periods. 2) Both spring/early-summer and late-summer adult populations of *sathon* evidently occur. 3) The records for *univittatus* comprise the October–December period and a rearing record in May, so there may be two populations of adults per year. 4) If *sathon* is omitted, the members of the *brevirostris* group are mid-summer emergent, whereas the *intermedius*-group species are mainly spring to early-summer emergent.

TABLE 2

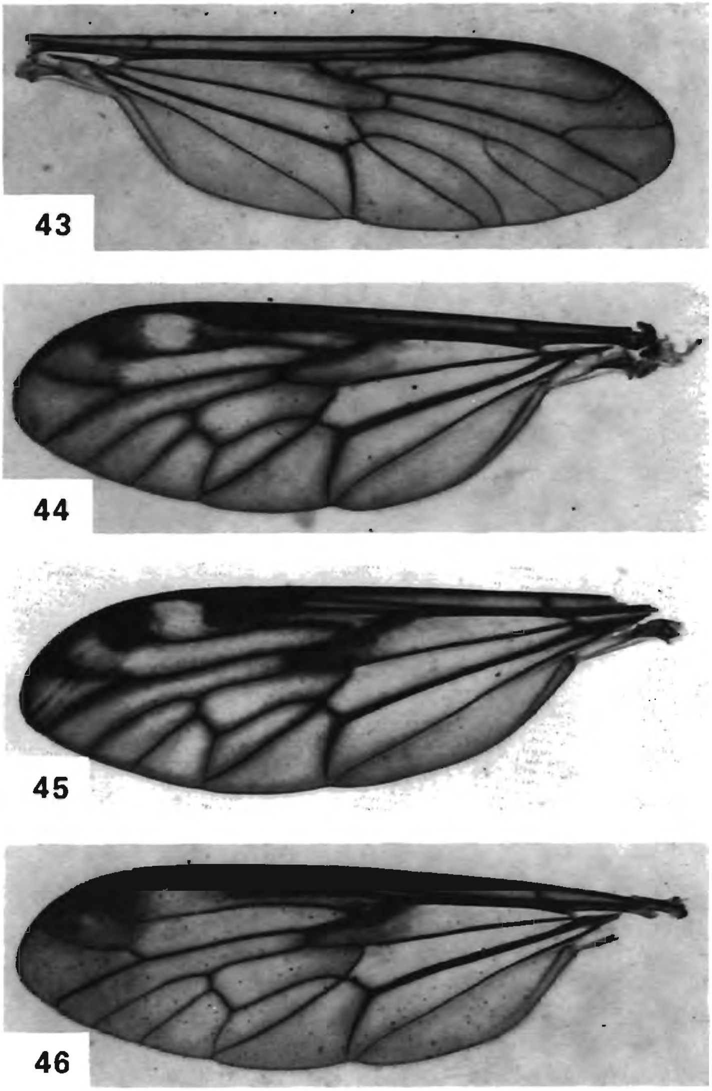
Phenology of *Vermipardus* flies, derived from label data and rearing records; any month for which there is only a record based on a reared specimen, is marked with x.

	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY
brincki							★	★	★			
promontorii				★			★					
basuto					★		★					
intermedius				★	★	★						
sylphe					x							
univittatus					x	★	★					x
brevirostris								x				
munroi								★	★			
londti							★	★				
sathon					★						★	

The requirements of the larvae resemble those of other vermileonid genera, especially in that there should be dry, loose, smoothly-granulated sand or sandy soil,



Figs 38–42. Wings of *Vermipardus* species. 38. *V. promontorii* (Stuckenberg). 39. *V. brincki* (Stuckenberg). 40. *V. intermedius* (Stuckenberg). 41. *V. univittatus* (Stuckenberg). 42. *V. basuto* (Stuckenberg).



Figs 43–46. Wings of *Vermipardus* species. 43. *V. sylphe* sp. n. 44. *V. londti* sp. n. 45. *V. sathon* sp. n. 46. *V. munroi* sp. n.

even of soft, dust-like or powdery fineness, for their pit-making. Although this suggests that *Vermipardus* species may favour arid environments where such material tends to be common, the known distribution of the genus indicates that these flies actually require breeding sites that are humid and shaded. The species are all recorded from montane areas or from topographically diversified terrain, in regions of relatively high rainfall. The larval habitat is always under some sort of shelter – typically the dry sandy floor under a rocky overhang or in a cave, or in a recess in an earthen bank. I have never found *Vermipardus* larvae under the sky or in a situation where they are openly exposed to rain. There is also a preference for such sites to be well shaded, particularly as a result of aspect (south-facing especially) and the presence of sheltering vegetation.

Sites with such a combination of features may be relatively uncommon and scattered in any locality. This became apparent during a search I made along more than one kilometre of both banks of the Rensburgspruit, a river in valley-bushveld near Estcourt in Natal. Although numerous recesses were found in the banks, nearly all were occupied by antlions (Neuroptera, Myrmeleontidae). Only one small wormlion population (about 20 pits of *brevirostris*) could be found; this had exclusive occupation of a sandy recess in a south-east facing bank at about one metre above ground-level, in a distinctive site where a thicket of trees and bushes provided exceptionally continuous and complete shade.

An examination of larval populations of *sylphe* proved particularly instructive. The type-locality, Fairy Glen in the Royal Natal National Park, is a small patch of quite dense *Podocarpus* forest in a little valley surrounded by extensive grassland. Within this forest, the larvae were restricted to a permanently shaded, quite dark recess beneath a small sandstone cliff, adjacent to a permanent mountain stream, where the air was continuously cool and humid. A search for this species was also made several kilometres away, along a path traversing a narrow strip of forest above a bank of the Thukela River below Tendele Camp. This forest is enclosed by extensive grassland. A solitary cluster of three larvae in a saucer-sized niche was found in the earthen bank bordering the path; recesses at ground-level all contained antlions. The flies apparently move from one forest patch to another, in search of the sporadic and isolated sites that meet the special needs of their larvae.

Are the larvae unselective predators? The old European literature accords *Vermileo* a reputation as a consumer of ants, and there is a belief prevalent that ants feature in the diet of vermileonids in general. Wheeler (1930) considered that the *Vermileo* species in California probably consume mostly ants; he also recorded rearing *Vermileo* and *Lampromyia* larvae on worker termites, aphids, and small caterpillars, as well as ants. Hemmingsen (1968) reared larvae of both genera on ants; other authors have resorted to flies as larval food, including houseflies, calliphorids, drosophilids and mosquitoes. I recorded a larva of *Vermipardus promontorii* overcoming a polydesmid millipede 30 mm long, and also *Dermestes* beetles 6 mm long (Stuckenberg 1961). *Vermipardus* larvae which I am rearing at the time of writing are being fed mostly houseflies; small spiders, isopods, and termite alates and workers, have also been fed to them successfully. Such records suggest that wormlions may consume any arthropod that falls into their pits, provided it is not too large, too heavily sclerotised, well-protected chemically, or formidably aggressive. Nevertheless, the unusual microhabitat occupied by *Vermipardus* larvae must limit the range of potential prey.

I was once surprised to find some empty carcases of muscid flies next to pits of *univittatus* in the large larval colony at Giant's Castle (described below); Hemmingsen (1968) noted this, but it was not certain that those flies had been prey. In an attempt to get more information, I revisited the site recently and removed about 125 cc of the fine, dusty sand in which many successive generations of wormlions had lived. This sample was shaken up in water, and the abundant debris that floated to the surface was skimmed off, dried, and examined under a stereoscopic microscope. Most of it was old, comminuted plant material. The following arthropod remains were found: **Coleoptera** – head of a small elaterid-like beetle; fragments of a small beetle; hindleg from chrysomelid-like beetle; two incomplete carcases of a mordellid-like species; thorax and leg-parts of a small, metallic-green beetle; pale orange elytra from at least six individuals of a small species of beetle. **Hymenoptera** – ant head of medium size; four abdomens and various legs of a small species of black ant; mandible of larger ant; small hindwing. **Homoptera** – carcase of small cicadellid-like nymph; small hindwing. **Diptera** – carcase of black sepsid fly; part of wing. **Arachnida** – carcase of immature ixodid tick; carcase of large terrestrial mite; part of spider's leg. **Miscellaneous** – some very small brown insect femora; indeterminate fragments of insect cuticle.

If these remains represent prey, and if they constitute a fair sample, the following conclusions can be drawn: 1) The remains are from small arthropods, which is to be expected as the prey must be of a size within the capacity of the wormlions in different instars to overcome them. 2) Coleopteran remains are more numerous and diverse than those of any other insect order; in part, this could reflect the suitability of the surrounding forest as a habitat for many small species of beetles. 3) Ants constitute part of the food resource, but in that montane forest, at an altitude of about 1675 m, ants are inconspicuous and cryptic so may not commonly be available as prey. 4) Opportunism is suggested by the diverse arachnid, dipteran and homopteran remains. The data suggest that these wormlions are indeed impartial predators of small arthropods.

The ethological convergence between antlions and wormlions is well known: certain myrmeleontid taxa (in South Africa, species of the genera *Hagenomyia*, *Cueta* and *Myrmeleon* – Mansell 1985) also make pitfall-traps in sand. Hemmingsen (1963) describes the convergence as follows: '...the construction in sand of pits for traps; lying in wait at the bottom; pulling down the seized prey into the sand; and using the head to throw up sand, when digging, to confuse escaping prey, and later to throw up abandoned prey. The two groups have also in common extra-oral digestion and closing off of the passage between mid- and hind-intestine, various sensory reactions and taxes, death feigning, the ability to starve for months, pupation in the sand and movement of the pupa to the surface before emergence.' During my search for wormlions, I sifted out the inhabitants of numerous pit aggregations but almost invariably found only antlions. My experience in Natal has been that the great majority of pits at ground-level in sheltered sites are occupied by antlions. At Fairy Glen there was a particularly interesting situation: larvae of *sylphe* occurred only in pockets of fine sand on small rock-ledges about one metre above ground-level. On these ledges no antlions were found, but they were numerous at ground-level below the ledges, wherever there were patches of sand. Spatial separation was clearly evident in the two occupation levels.

The other Natal Drakensberg species, *univittatus*, differs in utilising accumulations of fine sand at ground-level under rocky overhangs or in caves, provided there is continuous shade. In the riverine forest near Main Cave in the Giant's Castle Reserve, the floor of a large sloping recess, beneath a massive boulder close to the river, is known by me to have been occupied by a substantial larval population of this species for at least 40 years. Much smaller colonies of larvae occur sporadically under sloping rocks nearby within the forest; one colony occupies powdery soil in a gloomy, perhumid recess at the side of a waterfall in a small ravine. No pit-building antlions have been found yet in this forest. I did find, however, among the organic debris sampled from the large larval colony of *univittatus*, a very small live myrmeleontid larva. This antlion proved to be of a species that does not construct pits; Dr M. Mansell (*in litt.*) has identified it as *Tricholeon hirtellus* Esben-Petersen, which he informs me is common in sand accumulations on rocky ledges in the Drakensberg. If more of these antlions are present, presumably they have to live near the surface between the wormlion pits, and will be in competition for space and prey in the shelter.

A different situation was found at the Krantzkloof Nature Reserve near Durban. A search I made of a thickly-wooded gorge revealed a large recess, about 20 m long, in the base of a horizontal sandstone ridge on the bank of a permanent stream. The floor of this recess contained numerous pits irregularly clustered relative to the depth and distribution of sand. Most of the pits were occupied by antlions; only in one small area was there a cluster of pits inhabited by wormlions (species unknown, not yet metamorphosed). Several small caves and overhangs nearby had only antlions present.

These preliminary observations raise certain questions: 1) Are differences in larval requirements the cause of the apparent rarity of sites shared by wormlions and antlions? 2) Are wormlions excluded from suitable sites by the presence of antlions? 3) Does predation by antlions on wormlions occur, and is it a limiting factor? These are moot points, and further study is warranted. The case of *sylphe* could be an instance of resource-partitioning whereby predation is avoided.

CLADISTICS AND BIOGEOGRAPHY OF *VERMIPARDUS*

Three impediments exist in presenting a satisfactory account of the biogeography of these wormlion flies. First, there are probably still undiscovered species, to the extent that new discoveries may radically transform the patterns of distribution known at present. Second, it is still not possible to present a cladogram including all three of the species-groups as a rooted, fully-resolved tree. Third, although the species-groups are clearly distinguishable, only the *brevirostris* group can confidently be demonstrated to be monophyletic by means of morphological apomorphies. The *intermedius* group is almost certainly monophyletic, but is defined at present mainly on features of colouring and pattern. The *promontorii* group includes two species of closely similar appearance, but (see above) there are some character-states in both species that suggest that each may be related to species in one of the other groups. There is no satisfactory way of basing a cladistic study on colouring and pattern in this genus, even though these features are as much expressions of the genotype as morphological characters are. The polarity of such characters is indeterminate, and reference to outgroups (in this case, *Lampromyia* and *Vermilynx*) is unhelpful. The best that can be done is to assume that the monophyly of these groups is indeed demonstrated by the characters used for their definition, and to see what biogeographical conclusions can be drawn.

Fig. 49 shows the distribution of the three groups in South Africa. The large gap between the Natal and Eastern Cape areas occupied by species of the *brevirostris* group is surely due to incomplete collecting. Similarly, the area between the Cape Peninsula and the most western record for *londti* may in fact be occupied by species still undiscovered.

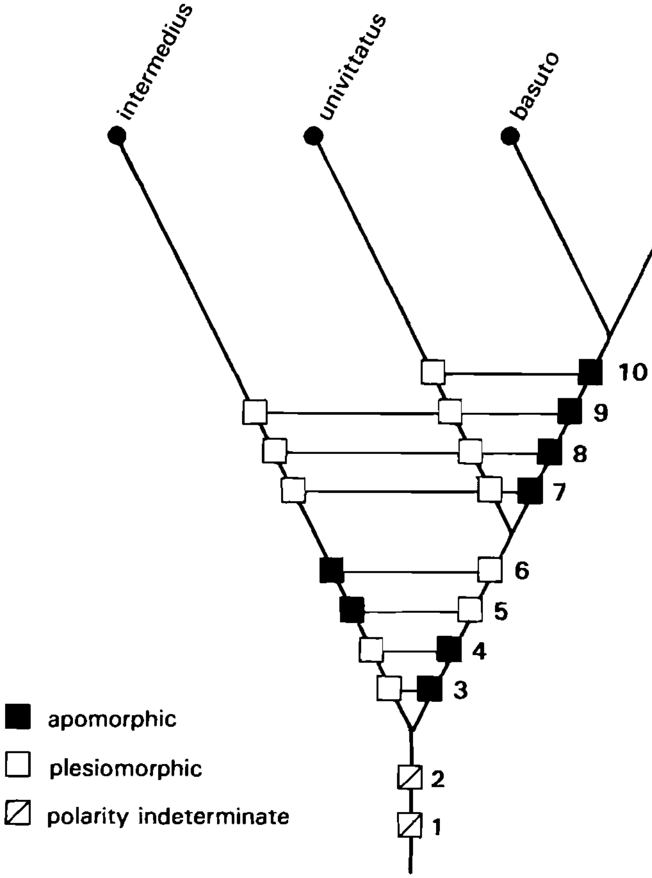


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Fig. 47. Cladogram for the *intermedius* group; the characters used are listed in the Appendix.

***promontorii* group**: The occurrence of two similar species of *Vermipardus* on the Cape Peninsula could be a further instance of the localised speciation and endemism for which the biota of this relatively small (*ca.* 300 sq. km.) but topographically complex and extremely rugged promontory are renowned. There are too few records to judge whether these species may be sympatric anywhere. Both *Lampromyia sericea* (Westwood) and *L. appendiculata* Bezzi also occur on the Cape Peninsula (unpublished records, specimens in NMSA), so this spur of land, with four species in two genera, has the world's largest concentration of vermileonids.

***intermedius* group**: A cladogram for the species (Figs 47, 50) can be expressed as follows: *intermedius* + (*univittatus* + (*basuto* + *sylphe*)). This can be translated into the following area cladogram: Fish River Basin + (Escarpment + (Lesotho Interior + Mont-aux-Sources)). 'Escarpment' refers to the Great Escarpment in its Natal and Eastern Cape sections, as well as the southern topographic outliers of the Winterberg and Amatola Ranges. The species *sylphe* is known only from Mont-aux-Sources at the northern end of the main Drakensberg escarpment in Natal; this is surprising as the Drakensberg, extending south-west from there towards Giant's Castle, presents no evident change in geomorphology or environmental factors that would prevent sympatry by *sylphe* and *univittatus*. It is possible that the distribution of *sylphe* may extend north of the high Lesotho terrain, via the Golden Gate highlands; this would offer the possibility of a former distribution of the species ancestral to *sylphe* + *basuto* from the Lesotho interior to the Mont-aux- Sources area (see below).

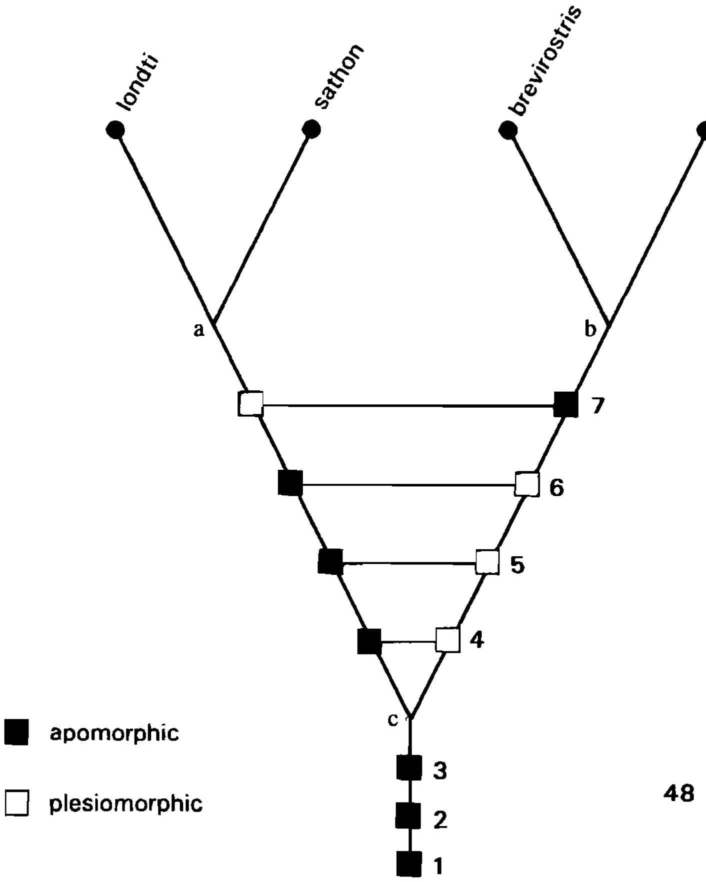

Fig. 48. Cladogram for the *brevirostris* group; the characters used are listed in the Appendix.

***brevirostris* group**: The cladogram (Figs 48, 51) reveals the following situation: (*sathon* + *londti*) + (*brevirostris* + *munroi*). The relationships of the four species are obvious, but they yield an unexpected area cladogram: *sathon* and *brevirostris* evidently occupy valley-bushveld in adjacent river basins in the middle of Natal, but they belong to different species-pairs; their respective sister-species, *londti* and *munroi*, exist in the Eastern Cape Province. Given this clear pattern of relationships, the taxon cladogram has hypothetical ancestral taxa at nodes 'a' and 'b'; both gave rise to a valley-bushveld species in Natal and to a coastal hinterland species in the Eastern Cape Province. Nodes 'a' and 'b' in the area cladogram also represent events that promoted speciation, but it is not apparent what these might have been. At node 'c' an earlier hypothetical ancestor is represented, about which nothing can be inferred.

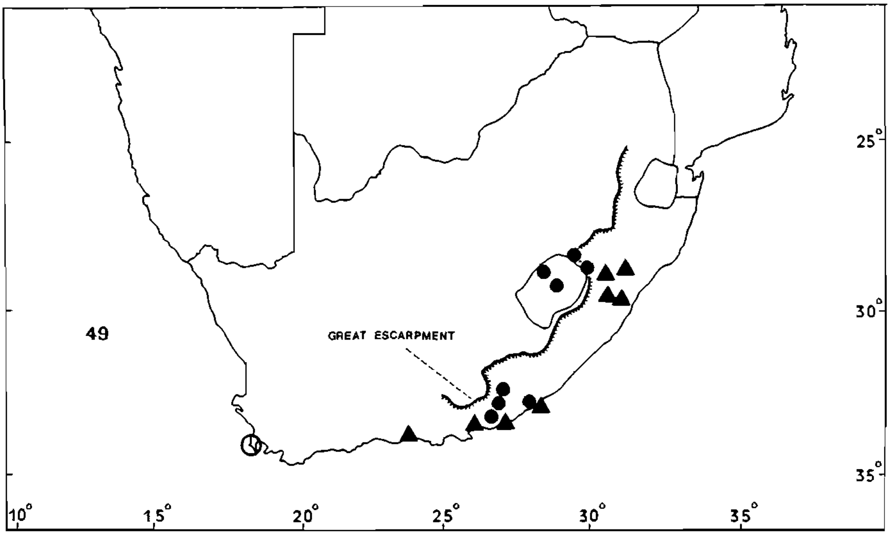

Fig. 49. Distribution of species-groups in South Africa: ○ = *promontorii* group (Cape Peninsula); ● = *intermedius* group; ▲ = *brevirostris* group. The position of the Great Escarpment in the Eastern Cape Province and Natal is indicated.

Historical biogeography: Considering only the *intermedius* and *brevirostris* groups, it is evident that their distribution and cladogenesis are clearly associated with (a) the Great Escarpment, and (b) the eastern and south-eastern slopes between the Great Escarpment and the Indian Ocean seaboard. The following discussion is based extensively on the seminal account of Southern African geomorphological history by Partridge & Maud (1987).

The Great Escarpment (Fig. 49) is '..arguably the single most important geomorphic feature of the subcontinent' (Partridge & Maud 1987), as it separates the elevated interior plateau from the lower-lying peripheral slopes. It is an ancient feature, whose genesis lay in continental rifting during the breakup of Gondwanaland in the late Jurassic or early Cretaceous. Its survival up to the present was due largely to the presence of high elevations in eastern South Africa consequent upon the original position of Southern Africa in central Gondwanaland. Following rifting and the formation of the eastern seaboard, an immensely long cycle of erosion (more than 100 Ma) followed, which terminated only in the early Miocene. Most of the erosion and scarp recession occurred during the earlier part of this cycle, and it had virtually ceased by the Oligocene when interior planation was far advanced and the subcontinent '..had been reduced to a vast, undulating plain punctuated at infrequent intervals by erosional residuals and high-lying massifs' (Partridge & Maud 1987). In the early Miocene, moderate uplift tilted the subcontinent slightly to the west and started a new landscape cycle which terminated near the end of the Pliocene. A second uplift, but of major proportions (as much as 900 m), then raised the interior along a Ciskei-Swaziland axis just east of the present position of the Drakensberg, and led to a vigorous erosion cycle that produced the deep incision of river systems on the coastal hinterland of south-eastern South Africa that characterises the present-day topography.

Early in the period following continental rifting, a drainage system evolved that produced a seaward-facing erosional face close to and more or less parallel with the south-eastern coast. This was the forerunner of the Great Escarpment. By the end of the Cretaceous, the Great Escarpment had eroded to a position not far eastward of its present position in Natal and the Eastern Cape. The two subsequent erosion cycles, initiated in the late Early Miocene and the Pliocene, resulted in further backwearing of a few tens of kilometres.

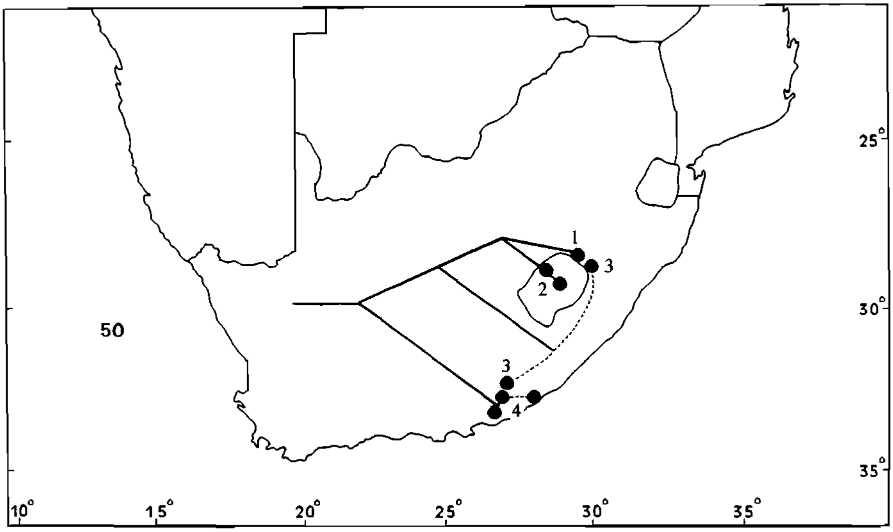

Fig. 50. Distribution of *intermedius* clade: 1 = *sylphe*, 2 = *basuto*, 3 = *univittatus*, 4 = *intermedius*.

At the end of the Jurassic, rocks of the Karoo Supergroup covered most of South Africa, with the notable exception of the region occupied by the Cape Fold Mountains which are of Permian-Triassic age (Halbich *et al.* 1983). This immensely thick sequence of almost horizontal strata would thus, from virtually the outset, have influenced and determined the evolution of topography as backcutting erosion and scarp recession proceeded in south-eastern South Africa. The type of geomorphology typical of the Natal Drakensberg would soon have appeared as the form of the Great Escarpment emerged; this would have been a consequence of underpinning by erosion-resistant sandstone ('Cave Sandstone') of the Clarens Group and the presence of the massive terminal sequence of volcanic lavas above. Because of the uniform horizontality of strata over great distances, there would have been endlessly repeated landscapes – of enormous foothills layered with sandstone, extending generally eastwards, surmounted by high escarpment cliffs of lavas – like those characteristic of Drakensberg scenery today. This would always have been the terrain with the highest and most reliable rainfall. In short, the Great Escarpment offered topographic and ecological conditions of great uniformity and continuity over an immense period of post-Jurassic time. Uplift in the Pliocene was sufficient to have affected the climate of the Great Escarpment significantly in the direction of lower temperatures and greater seasonal contrasts.

The eastern slopes between the Great Escarpment and the sea would have diversified topographically, and hence ecologically, as erosion deepened through the underlying Beaufort, Ecca and Dwyka strata of the Karoo Supergroup and exposed the older formations beneath. Exposure of dolerite dykes and sills, and of erosion-resistant sandstone on the coast of Pondoland and in southern Natal, produced distinctive and in places elevated topography. The Pliocene uplift then rejuvenated river erosion and accentuated topographic diversification through downcutting into the old scarps, valleys and plains left by the less significant Miocene uplift. The flora probably evolved a comparable diversity in response to greater variability in ecological conditions on the slopes between the escarpment and the sea. Finally, during the Pleistocene glacial maxima, severe periglacial conditions occurred in the upper reaches of the escarpment and the uplands of Lesotho (Lewis 1988), and would have impacted on the biota there; the effects of these cold, dry cycles on the eastern slopes is still unclear.

Given this enormously long period of landscape evolution in eastern South Africa, with so few tectonic interruptions, the question of estimating the time of first occupation by vermileonids is problematical. Although a Jurassic origin for the Vermileonidae is probable, Eurasian fossil wings from that epoch which have been attributed to this family (Hennig 1954 1967; Kovalev 1987) are, in my view, not indisputably vermileonids. The only definite dating evidence is provided by the Baltic amber fossil *Protovermileo electricus* Hennig (1967), but the age of Baltic amber is uncertain, with the range of 55–35 Ma (earliest Eocene to mid-Oligocene) being conservatively estimated (Larsson 1978). As *Protovermileo* is close to the extant genus *Vermileo*, it is probable that the Recent vermileonid genera had evolved by the end of the Cretaceous. The Afrotropical genera would have diversified from ancestral stock that responded to Cretaceous floral evolution by evolving the elongate proboscis unique to these genera.

Although Vermileonidae must be an old group in South Africa, it is notable that species allopatry is evident throughout the range of the family in this region. I know of no locality in South Africa where two species of vermileonids (even of different genera) occur together. This suggests that dispersal is uncommon, very slow, or limited in effectiveness, and that vicariant speciation has been operative.

The sort of habitat in the Drakensberg occupied by *intermedius* group species may be close to the ancestral habitat of the genus. Following a hot, humid climatic regime during the late Cretaceous, a warm, mesic environment prevailed in eastern South Africa in the Palaeogene and until the mid-Miocene (Maud & Partridge 1987). It may be assumed that forest occurred extensively in the Great Escarpment foothills during that time. Van Wyk (1990) states: 'In the late Cretaceous-Palaeocene, subtropical rainforest prevailed in the lowland regions of the present-day Natal/Cape Region.' Differentiation of the *brevirostris* group probably represented a cladogenetic response to opportunities offered by the evolution of drier woodlands in the deepening river basins between the escarpment and the coast.

Vicariance resulting in the evolution of the *univittatus* + (*basuto* + *sylphe*) clade cannot presently be fully explained. It seems probable that the separation of the ancestral *intermedius* population was associated with the development of the Fish River basin south of the Great Escarpment. This river basin is of sufficient antiquity and topographic significance to have developed as a biogeographical entity in its own right, as well as a barrier between the south-eastern end of the Great Escarpment and the easternmost termination of the Cape Fold Mountains near Grahamstown (Stuckenberg 1962). The Fish River was established as an original element of the early Cretaceous drainage, and no datable event can be linked at present to this vicariance. Cladogensis within the *brevirostris* group may be dated to later Miocene, if it is correct that the species in Natal are restricted to adjacent river basins accentuated as a result of the early Miocene uplift.

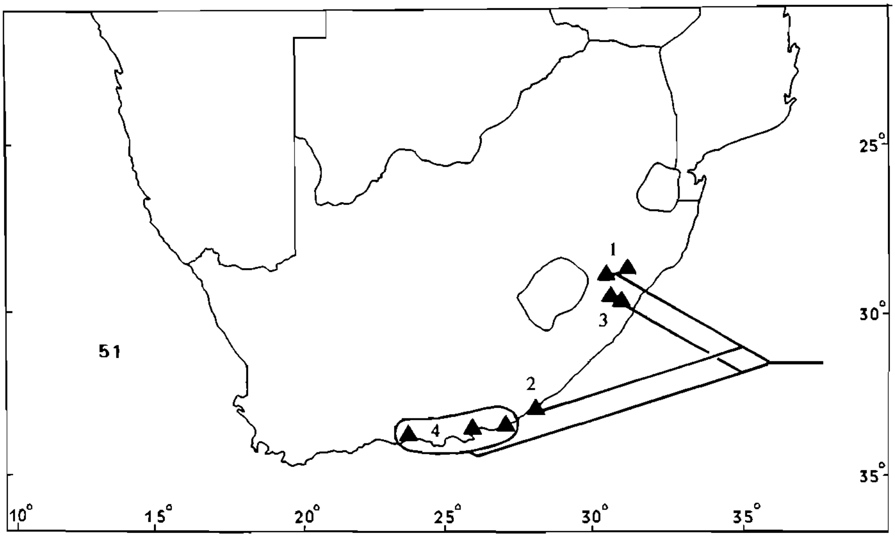

Fig. 51. Distribution of *brevirostris* clade: 1 = *brevirostris*, 2 = *munroi*, 3 = *sathon*, 4 = *londti*.

The biogeography of *Vermipardus* can be compared with the distribution of the South African Notonemouridae (Plecoptera) mapped recently by Stevens & Picker (1995). These authors present no cladogram for the notonemourid genera, so no area cladogram can be inferred. Nevertheless, it is notable that this aquatic group, tied to mountain streams, has a clade (the genus *Balinskycercella* Stevens & Picker) which is equivalent to and geographically congruent with the *basuto* + *sylphe* pair in *Vermipardus*. Two of the three species of *Balinskycercella* (*fontium* and *tugelae*) occur at Mont-aux-Sources, the type-locality of *sylphe*; *B. tugelae* occurs also in northern Lesotho where the third species *B. gudu* occurs. Thus, in aquatic and terrestrial families, in separate insect orders, the vicariance dichotomy of Northern Lesotho + Mont-aux-Sources is found; this is an endem-centre not previously recognised in South African palaeogenic invertebrates. Its limits in Lesotho are still uncertain; it probably occupies much of the Maloti Range and lesser ranges in the northern, north-western and central parts. At the northern end it may extend via the Golden Gate highlands to the Mont-aux-Sources area and the Royal Natal National Park, where the Golden Gate highlands and the High ('Quathlambia') Drakensberg of Natal intergrade. The bleak alpine zone along the summit of the Drakensberg evidently constitutes a climatic barrier to faunal exchange between the Lesotho interior and the Great Escarpment in Natal. This zone would have been formed initially as a result of the end-Pliocene uplift, so vicariant speciation in this endem-centre may be post-Pliocene.

The notonemourid genus *Afronemoura* Illies is substantially equivalent to the *brevirostris* group, ranging from the Amatola mountains through a series of localities between the Drakensberg and the coast in Natal, but also occurring in the Drakensberg escarpment of the Eastern Transvaal. It will be through the discovery of more such congruences among disparate taxa that a sound understanding of South African invertebrate biogeography can be attained.

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APPENDIX

Character states used in construction of cladograms (Figs 46, 47); (A) = apomorphic condition, (P) = plesiomorphic condition.

Fig. 47: *intermedius* group

1. Body mainly reddish or yellowish-brown; species in other groups have other colourations, but polarity is indeterminate.
2. All legs more or less unicolorous; the contrasting colouring of hind legs in *brevirostris* group may be an apomorphy, but polarity is indeterminate at present.
3. Spiculae present on aedeagal shaft (A); spiculae confined to aedeagal apex only (P); more extensive distribution of spiculae is interpreted as a specialised condition.
4. Gonostyle falcate (A); gonostyle straighter and more finger-like (P).
5. Wing patterned (A); wing plain (P).
6. R_{2+3} apically angled (A); curved forwards apically (P).
7. Dorsal bridge narrow (A); dorsal bridge larger (P).
8. Ventral aperture short and wide (A); ventral aperture narrow, elongate fusiform (P).

9. Apical guides broad, convergent (A); apical guides elongate, narrow, subparallel (P).
10. Aedeagus with sawtoothed lateral ridges (A); such ridges lacking (P).

Fig. 48: *brevirostris* group

1. Gonostyle bifid (A); gonostyle simple (P).
2. Transformation series associated with elongation of aedeagus and specialised form of dorsal bridge (A); plesiomorphic form of bridge is a simple transverse sclerotised band connecting dorsobasal margins of synsternite (P).
3. R_{2+3} flexed forwards apically (A); this vein curved forwards apically (P); an apomorphy independently evolved in some species of *Lampromyia*.
4. Dorsal bridge of highly specialised form (Figs 26, 32) (A); dorsal bridge simpler, less extended (Fig. 21) (P).
5. Aedeagus very elongate (A); aedeagus shorter, more similar to condition seen in other groups (P).
6. Aedeagus apically swollen (A); apex tapering or rounded (P).
7. Shaft of aedeagus ridged along each lower side, this ridge produced into conspicuous teeth at bend in shaft (A); such a condition undeveloped (P).

REFERENCES

BEZZI, M. 1926. South African Rhagionidae (Diptera) in the South African Museum. *Annals of the South African Museum* **23**: 297–324.

GRIFFITHS, G. C. D. 1994. Relationships among the major subgroups of Brachycera (Diptera): a critical review. *Canadian Entomologist* **126**: 861–880.

HALBICH, I. W., FITCH, F. J. AND MILLER, J. A. 1983. Dating the Cape orogeny. *Geological Society of South Africa Special Publication* **12**: 149–164.

HEMMINGSEN, A. M. 1963. The Ant-lion-like Sand Trap of the Larva of *Lampromyia canariensis* Macquart (Diptera, Leptidae=Rhagionidae, Vermileoninae). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* **125**: 237–267.

——— 1968. A review of instinctive behaviour in the worm-lions *Vermileo vermileo* L. and *Lampromyia pallida* Macquart (Diptera Brachycera, Rhagionidae, Vermileoninae). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* **131**: 289–302.

HENNIG, W. 1954. Flügelgeäder und System der Dipteren unter Berücksichtigung des aus dem Mesozoikum beschriebenen Fossilien. *Beiträge zur Entomologie* **4**: 245–388.

——— 1967. Die sogenannten "niederen Brachycera" im Baltischen Bernstein (Diptera: Fam. Xylophagidae, Xylomyidae, Rhagionidae, Tabanidae). *Stuttgarter Beiträge zur Naturkunde* **174**: 1–51.

KOVALEV, V. G. 1987. Classification of the Diptera in the light of Palaeontological Data. *In*: Narchuk, E. P. (ed.), *Two-winged Insects: Systematics, Morphology and Ecology*. Leningrad: Zoological Institute of USSR Academy of Sciences pp. 40–48.

LARSSON, S. G. 1978. Baltic Amber – a Palaeobiological Study. Klampenborg: Scandinavian Science Press. *Entomonograph* **1**.

LEWIS, C. A. 1988. Periglacial features in southern Africa: A review, 1987. *Palaeoecology of Africa* **19**: 357–370.

MANSELL, M. W. 1985. [Chapter] 19. Neuroptera. *In*: Scholtz, C. H. & Holm, E. (eds.), *Insects of Southern Africa*. Durban: Butterworths p. 186.

MAUD, R. R. & PARTRIDGE, T. C. 1987. Regional geomorphic evidence for climatic change in Southern Africa since the Mesozoic. *Palaeoecology of Africa* **18**: 337–348.

NAGATOMI, A. 1977. Classification of Lower Brachycera (Diptera). *Journal of Natural History* **11**: 321–335.

PARTRIDGE, T. C. AND MAUD, R. R. 1987. Geomorphic evolution of southern Africa since the Mesozoic. *South African Journal of Geology* **90**: 179–208.

STEVENS, D. M. & PICKER, M. D. 1995. The Notonemouridae (Plecoptera) of southern Africa: description of a new genus, *Balinskycercella*, and a key to genera. *African Entomology* **3**: 77–83.

STUCKENBERG, B. R. 1955. New and little-known South African Rhagionidae (Diptera). *Journal of the Entomological Society of Southern Africa* **18**: 255–265.

——— 1960. Diptera (Brachycera) Rhagionidae. *In*: Hanström, B., Brinck, P. & Rudebeck, G. (eds.), *South African Animal Life* **7**. Stockholm: Swedish Natural Science Research Council pp. 216–308.

——— 1961. Records and descriptions of Blepharoceridae, Erinnidae and Rhagionidae from South Africa (Diptera). *Annals of the Natal Museum* **15**: 109–124.

——— 1962. The distribution of the montane palaeogenic element in the South African invertebrate fauna. *Annals of the Cape Provincial Museums* **2**: 190–205.

——— 1965. A new species of *Lampromyia* Macquart (Diptera: Rhagionidae) from the Richtersveld. *Journal of the Entomological Society of Southern Africa* **28**: 107–109.

——— 1995. *Vermilynx*, a new genus for the wormlion fly *Lampromyia vansoni* Stuckenberg of the Richtersveld, southern Africa (Diptera: Vermileonidae). *African Entomology* **3**: 29–34.

VAN WYK, A. E. 1990. The sandstone regions of Natal and Pondoland: Remarkable centres of endemism. *Palaeoecology of Africa* **21**: 243–257.

WHEELER, W. M. 1930. *Demons of the Dust*. London: Kegan Paul, Trench, Trubner & Co., Ltd.

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